

# Spatial effects of artificial feeders on hummingbird abundance, floral visitation and pollen deposition

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**Abstract** Providing hummingbirds with artificial feeders containing sugar solution is common practice throughout the Americas. Although feeders can affect hummingbird foraging behavior and abundance, it is poorly understood how far this effect may extend. Moreover, it remains debated whether nectar-feeders have a negative impact on hummingbird-pollinated plants by reducing flower visitation rates and pollen transfer close to the feeders. Here, we investigated the effects of distance to nectar-feeders on a local hummingbird assemblage and the pollination of *Psychotria nuda* (Rubiaceae), a hummingbird-pollinated plant endemic to the Brazilian Atlantic Rainforest. At increasing distance (0–1000 m) from a feeding-station, where hummingbirds have been fed continuously for the past 13 years, we quantified hummingbird abundance, and rates of flower visitation and pollen deposition on *P. nuda*.

We found that hummingbird abundance was unrelated to distance from the feeders beyond ca. 75 m, but increased steeply closer to the feeders; the only exception was the small hummingbird *Phaethornis ruber*, which remained absent from the feeders. Plants of *P. nuda* within ca. 125 m from the feeders received increasingly more visits, coinciding with the higher hummingbird abundance, whereas visitation rate beyond 125 m showed no distance-related trend. Despite this, pollen deposition was not associated with distance from the feeders. Our findings illustrate that artificial nectar-feeders may locally increase hummingbird abundance, and possibly affect species composition and pollination redundancy, without necessarily having a disruptive effect on pollination services and plants' reproductive fitness. This may apply not only to hummingbirds, but also to other animal pollinators.

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## Zusammenfassung

### Bruterfolg bei der Kohlmeise und ihr Zusammenhang mit Eigenschaften natürlicher Nisthöhlen in einem Urwald

Das Angebot künstlicher Nektarspender gefüllt mit Zuckerklösung für Kolibris ist eine gängige Praxis in ganz Nord-, Mittel- und Südamerika. Obwohl die Nektarspender das Nahrungssuchverhalten von Kolibris beeinflussen können, ist wenig bekannt über das Ausmaß dieses Effektes. Vielmehr ist zu überlegen, ob Nektarspender nicht negative Auswirkungen auf durch Kolibris bestäubte Pflanzen durch weniger Blütenbesuche und verringertem Pollentransfer in

der Nähe der Futterstellen haben. Wir untersuchten die Effekte der Entfernung zu Nektarspendern in einer lokalen Kolibrigemeinschaft und die Bestäubung von *Psychotria nuda* (Rubiaceae), eine durch Kolibris bestäubte, endemische Pflanze im atlantischen Regenwald von Brasilien. Mit ansteigender Distanz (0–1000 m) zu einer Futterstelle, wo Kolibris seit 13 Jahren kontinuierlich gefüttert werden, quantifizierten wir die Kolibriddichte sowie die Raten der Blütenbesuche und Pollenverbreitung von *P. nuda*. Es zeigte sich, dass die Dichte von Kolibris nicht verbunden war mit einer Entfernung von über ca. 75 m zu Futterstellen, stieg jedoch stark an in der Nähe von Futterstellen. Die einzige Ausnahme bildete die kleine Art *Phaethornis ruber*, die nicht an den Futterstellen anwesend war. *P. nuda* Pflanzen innerhalb von ca. 125 m zu den Nektarspendern wurden zunehmend mehr besucht, einhergehend mit einer höheren Kolibriddichte, wobei die Besuchsrate jenseits von 125 m keinen distanzbezogenen Trend zeigte. Trotz dieser Beobachtung war die Pollenverbreitung nicht assoziiert mit der Entfernung zu den Futterstellen. Unsere Ergebnisse zeigen, dass künstliche Nektarspender lokal die Kolibriddichte erhöhen können und möglicherweise auch die Artenzusammensetzung verändern. Sie müssen aber nicht zwangsläufig einen störenden Effekt auf die Bestäubungsleistung von Kolibris und die reproduktive Fitness der Pflanzen haben.

## Introduction

Within the class Aves, and arguably across the vertebrates as a whole, hummingbirds exhibit the most specialized morphological and behavioral adaptations to nectar feeding (Feinsinger and Colwell 1978; Stiles 1981; Nicolson and Fleming 2003; Cronk and Ojeda 2008). Adaptations such as bill shape, specialized tongue, small body size, and the ability to hover are presumably the results of a long co-evolutionary history with the hundreds of flowering plants that depend on hummingbirds to mediate pollen transfer (Feinsinger and Colwell 1978; Martín González et al. 2015). Although not all hummingbird-visited plants fit the ornithophilous syndrome (e.g., Dalsgaard et al. 2009, 2012; Watts et al. 2012; Maruyama et al. 2013), many of these have tubular corollas, bright coloration, large amounts of dilute nectar, and lack scent as an attractant, i.e., are specialized toward hummingbirds (Cronk and Ojeda 2008; Dalsgaard et al. 2009). Thus, as local extinction of specialized avian pollinators may have a strong negative effect on the reproductive success of their plants (e.g., Anderson et al. 2011), changes in hummingbird species composition, abundances, and behavior could negatively affect plants specialized on hummingbird-pollination (Arizmendi et al. 2007).

Hummingbirds are popular among ornithologists and amateur naturalists due to their bright coloration, unique morphology and behavior. Hence, the use of artificial feeders filled with sugar solution has become a popular practice as they easily attract numerous hummingbird species (McCaffrey and Wethington 2008; Avalos et al. 2012; Brockmeyer and Schaefer 2012). In addition, artificial feeders have been used for research purposes; for instance, to study behavioral interactions (Maglianesi et al. 2015). In general, local hummingbird abundance appears to be limited by the availability of nectar (Montgomerie and Gass 1981); consequently, as feeders offer an unlimited resource of carbohydrates, they are often surrounded by a large number of individuals and species (Wethington and Russell 2003). A resulting hypothesis is that hummingbirds may reduce their visitation to local flowers, favoring feeders as they provide a more abundant and reliable resource, and thereby reducing pollen transfer among plants (Arizmendi et al. 2007; Avalos et al. 2012). Still, in years where floral abundance is high, nectar feeders may be less attractive to the hummingbirds, hence resulting in a negative association between floral abundance and feeder visitation rate (Inouye et al. 1991; McCaffrey and Wethington 2008). Despite its potential importance, few previous studies have focused on the consequences of nectar feeders, giving contradictory results. For instance, Arizmendi et al. (2007) showed that nectar feeders decreased visitation to nearby plants and reduced seed-set in one plant species in Mexico. In Costa Rica, Avalos et al. (2012) showed that near feeders ca. 50 % of all hummingbirds carried low or zero pollen loads, possibly because of reduced visitation to plants. In contrast, in the Andes, Brockmeyer and Schaefer (2012) found that feeders locally increased flower visitation, and, presumably, pollination of surrounding plants. Hence, previous work shows that feeders locally increase hummingbird abundance, but it is poorly understood how far this effect extends, i.e., how abundance changes with distance from feeders. Moreover, no consensus exists as to whether feeders have a negative or positive effect on the pollination of hummingbird-dependent plants.

Along a 1000-m transect in a Brazilian Atlantic Rainforest community, we evaluated how the presence of artificial nectar-feeders affects the local distribution of hummingbirds, and flower visitation and pollen deposition to *Psychotria nuda* (Rubiaceae), a hummingbird-pollinated plant endemic to the Brazilian Atlantic Rainforest. We used linear, quadratic and piecewise linear models to answer the following questions: (1) does the presence of feeders result in a local increase in hummingbird abundance? Specifically, we tested whether hummingbird abundance is only increased close to the feeders out to a threshold, or decreases linearly along the entire 1000-m transect; and (2) does floral visitation and pollen deposition decrease close to the feeders? The relevance of nectar-

feeders are discussed in relation to the ongoing anthropogenic changes in climate and land use also affecting pollination systems.

## Methods

### Study site and model plant

The study was carried out within 1 km of a private property called Folha Seca, in Ubatuba municipality, state of São Paulo, Southeastern Brazil (23°28′10″S–45°10′10″W). The property is situated within humid lowland rainforest at 15–25 m above sea level and borders the Serra do Mar State Park. The area is covered with primary forest that has been subjected to selective logging in the past. Mean annual temperature in the area is ca. 22 °C and annual rainfall is approx. 2600 mm (Sanchez et al. 1999). There are few other developed properties in the area, and these are situated such that they did not interrupt our study design. Folha Seca lies at the forest edge and more than 20 hummingbird species have been recorded there (J d’Abronzio, personal communication). The garden contains around a dozen feeders, which are refilled with sugar solution (~21 %) when empty, made from one part sucrose and four parts water. The owner of Folha Seca has been continuously feeding hummingbirds since 2001 and the daily consumption of sugar varies from ca. 1.5 to ca. 5 kg over the seasons, with the largest amounts consumed during the Austral winter. During our study period, ca. 2.0 kg of sugar was consumed on average per day. Hummingbirds drink most of the sugar solution, but other birds, including *Coereba flaveola*, *Chlorophanes spiza*, as well as several species of Hymenopterans (especially *Trigona* spp.), were also regularly observed on the feeders. We observed no mammals visiting the feeders at daytime, but did not examine if bats visited the feeders at night.

Our model plant, *Psychotria nuda* (Rubiaceae), is an understory flowering shrub, endemic to the Atlantic Rainforest in Brazil (Taylor et al. 2015). The species is largely ornithophilous, although insects such as *Bombus* spp. and *Heliconius* spp. may also visit its flowers (Castro and Araujo 2004). Flowers are ca. 2 cm in length, yellow, tubular with fused petals, which open diurnally and last 1 day. Nectar secretion accumulated over 9 h shows an average volume of  $12.0 \pm 5.7 \mu\text{l}$  and sugar concentration of  $16.5 \pm 7.4 \%$  (Castro and Araujo 2004). *P. nuda* is distylous with two distinct floral morphs occurring in sympatry, differing in the positioning of stigmas and anthers (Castro and Araujo 2004). In Folha Seca, the morph frequency ratio seems to be 1:1, but with a clumped spatial distribution (PK personal

observation). While the flowering phenology may vary geographically, a study conducted less than 50 km away from our location documented a flowering period between February and June, with a peak in April (Castro and Araujo 2004).

### Hummingbird abundance, floral visitation and pollen deposition

The data were collected in the peak flowering period of *P. nuda*, between 21 and 29 April 2014, and were centered within 1 km of the private residence of Folha Seca. In an east–west direction, skirting the garden on its southern side is a single-lane gravel road. The road runs through homogenous enclosed forest for 1.2 km to the east of the garden and 0.6 km to the west. The garden is somewhat isolated from the road by vegetation, but is connected to the road with a short driveway, which for this study we defined as zero meters from the feeders to ensure a similar vegetation type throughout the transect. In the western direction from the feeders, we located four points at 50, 150, 250 and 350 m, and to the east we placed ten points at 100, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 m. For each point, we identified the closest *P. nuda* having three or more open flowers. The distance to the nearest *P. nuda* never exceeded 20 m. For each point, we collected independent measures of hummingbird abundance, visitation rate, floral abundance and pollen deposition. Each morning, we monitored up to five randomly chosen sampling points with the condition of a minimum separated distance of 100 m to assure sufficient independence in hummingbird counts among sampling units. We collected two replicates for each sampling point. For the second sampling of visitation and pollen deposition, we chose a different plant if the point held more than one individual; otherwise, we collected from the same plant as earlier.

For each point replicate, at a distance of 25 m around the subject plants, we estimated the abundance of each hummingbird species by conducting 20 min point counts. This was done by one observer (JVB) who was experienced with the local avifauna. The point counts started early in the morning just after sunrise and proceeded in a randomized order until noon. All hummingbirds were identified to species level by sight and vocalizations. In order to minimize sampling biases, JVB discarded records suspected to be of a previously recorded individual, for instance, if a hummingbird held a territory. Due to the high density of hummingbirds around the feeders, it was not possible to use the same method for quantifying abundance. Instead, over 20 min periods, JVB recorded the maximum number of individuals of each hummingbird species observed at the same time, and repeated this sampling for eight consecutive days. Considering the floral

abundance of *P. nuda*, we counted all conspecific open flowers within a 10-m radius of the subject plant. Additionally, we counted all open flowers from other plant species in the area known to receive visits from hummingbirds such as *Nematanthus fritschii* (Gesneriaceae), *Hedychium coronarium* (Zingiberaceae) and *Stachytarpheta cayennensis* (Verbenaceae; Maruyama et al. 2015).

Hummingbird visitation rate to *P. nuda* was recorded in periods of 3 h, starting early morning after sunrise (approximately 07:00), and monitoring one plant at a time. We defined a visit as continuous feeding on the focal plant, ending with the bird flying away or perching nearby. The observations were either done by tripod-mounted cameras (Sony® HandyCam DCR-SR21 with long lasting batteries) or by direct observation. Except for a few plants that were unsuitable for camera monitoring, we randomized the placement of the different observers and cameras. At 12:00, from each of the focal plants, we randomly collected three to five flowers for estimation of pollen deposition. First, we extracted the style and stigma to keep the stigmas out of contact with the anthers. We then extracted deposited pollen from the stigmas using a piece of clear adhesive tape, which was lightly pressed three times on the stigma and afterwards placed on a glass slide. These were stored at ca. 6 °C for subsequent pollen counts. In the laboratory, the samples were stained using carmine red and pollen grains were counted using a microscope at  $\times 10$  magnification. The pollen of *P. nuda* is distinctively ornamented, which makes them easy to identify from other species (Castro and Araujo 2004). We omitted infertile pollen grains, identified by their small size, i.e.,  $\sim 25$   $\mu\text{m}$  in diameter in contrast to  $\sim 75$   $\mu\text{m}$  for normal sized grains.

### Statistical analyses

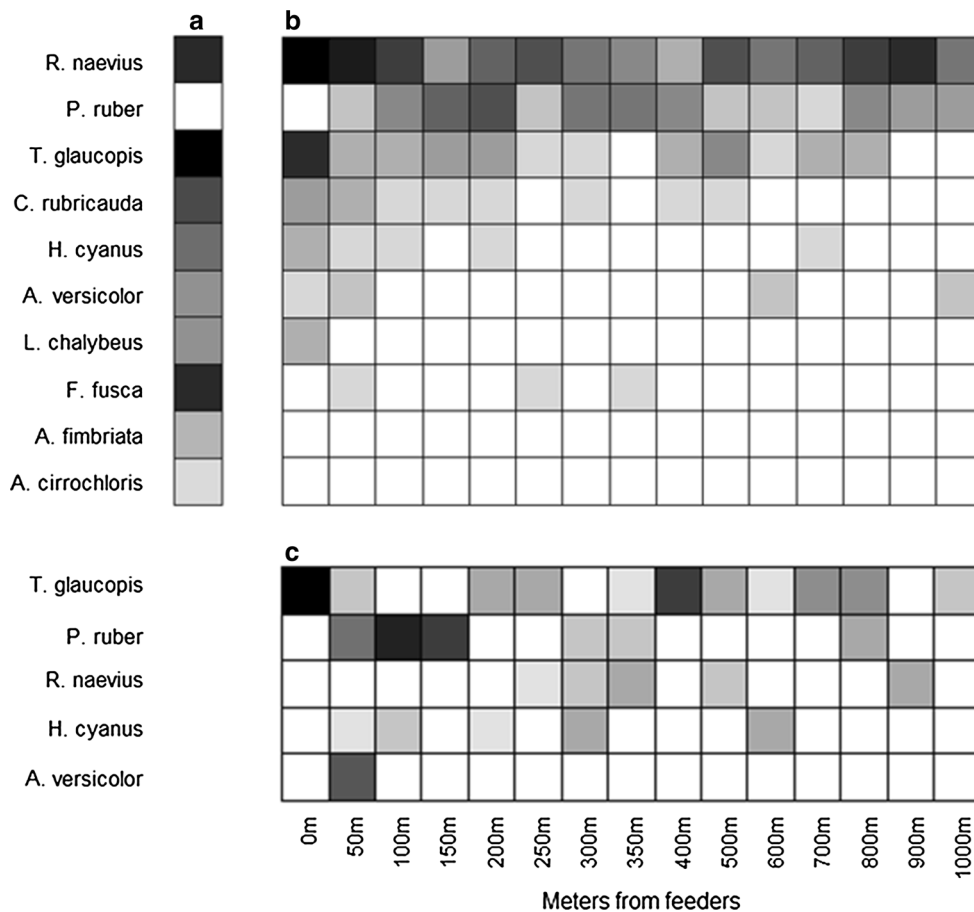
Using linear, quadratic and piecewise linear regression analyses, we tested if hummingbird abundance (individuals per 20 min; mean of two point counts), visitation rate (visiting individuals per 3 h; mean of two observation periods) and pollen deposition (number of pollen grains per flower; mean of two point samples) changed with increasing distance from the feeders. Specifically, we tested the following three different possible patterns: (1) decrease regularly throughout the 1000 m transect, i.e., linear relationship; (2) negative but curved association with distance, i.e., a quadratic association; and (3) strong linear effect at short distance from the feeders, but no effect beyond a certain threshold, i.e., piecewise linear relationship. As there was no difference in the median pollen deposition of the two floral morphs (Mann–Whitney test,  $U = 2062$ ,  $Z = 0.128$   $p = 0.898$ ), we did not distinguish between the morphs in our analyses.

The piecewise linear regression algorithm had to be supplied with one or more initial estimate parameters for the breakpoint ( $\psi_0$ ; i.e., the point where the regression slope is expected to change; Toms and Lesperance 2003, Muggeo 2008). After visual inspection of the data, we choose a distance of 200 m as the initial guess parameter. The fits of the linear, piecewise linear and quadratic models were compared to one another using the Akaike information criterion (AIC). We interpret the explained variation in the response variables based on  $R^2$  and the adjusted  $R^2$ .

To assess the influence of differences in habitat quality or attractiveness determined by community-level floral abundance, we fitted linear models for the abundance of *P. nuda* and other hummingbird-visited flowers around the focal *P. nuda* plants, against distance away from the feeders. Similarly, we used Spearman's correlation to test for associations between hummingbird visitation rates and both measures of flower abundance. Finally, to assess whether a distance related trend remained for visitation rate after accounting for hummingbird abundance (i.e., modeling visitation rate per individual hummingbird), we fitted linear, quadratic, and piecewise linear regression models to test for an association between distance and the residuals from a linear model predicting visitation rate by hummingbird abundance. All statistics were carried out using R version 3.1.1 (R Core Team 2014), and the piecewise regression analyses were conducted using the package "segmented" (Muggeo 2008).

### Results

We recorded ten species of hummingbirds, nine of which were recorded immediately around the feeders, the exception being *Phaethornis ruber*. Around the feeders, the most abundant species were *Thalurania glaucopis* (Mean  $\pm$  SD:  $7.4 \pm 1.2$  birds per 20 min), *Ramphodon naevius* ( $5.3 \pm 0.92$  birds per 20 min) and *Florisuga fusca* ( $5.3 \pm 0.9$  birds per 20 min; Fig. 1a). Hummingbird counts around the feeders recorded an average of 30 individuals (SD = 0.95 birds per 20 min;  $n = 8$  counting days). Along the transect, three species accounted for 87 % of records in our point counts (250 detections). Of these, by far the most common species was *R. naevius*, followed by the much smaller *Phaethornis ruber* and *T. glaucopis* (Fig. 1b). The remaining species recorded along the transect were: *Amazilia versicolor*, *Hylocharis cyanus*, *F. fusca*, *Lophornis chalybeus* and *Clytolaema rubricauda* (Fig. 1b). We recorded five species feeding on *P. nuda*, which were (in order of decreasing visitation frequency) *T. glaucopis*, *P. ruber*, *R. naevius*, *H. cyanus* and *A. versicolor*; visits of *T. glaucopis* represented nearly half of the records. The latter exhibited both generalist and territorial



**Fig. 1** Gray-scale schemes illustrating: **a** the averaged relative abundance of hummingbirds around the feeders (observations ranging from 0 to 7.4 birds per 20 min;  $n = 8$  counting days); **b** the averaged relative abundance along the 1000 m transect (observations ranging from 0 to 10 birds per 20 min;  $n = 2$  samplings per point); and **c** the averaged relative frequency of visitation rates along the transect (observations ranging from 0 to 11 birds per 20 min;  $n = 2$  samplings per point). For **a** and **b**, the hummingbird species have been sorted

vertically according to abundance along the transect and for **c**, according to the number of visits. *Dark shaded cells* illustrate high relative abundances/visitation rates; *white cells* illustrate absences. Feeders were situated approx. 20 m from the 0 m point of the transect (see “Methods” section). Note that *A. fimbriata* and *A. cirrochloris* were only observed at the feeders, whereas *P. ruber* was only observed along the transect

behavior (*sensu* Feinsinger and Colwell 1978). Indications of traplining behavior, i.e., birds following a repeated foraging circuit, were observed for the hermits *P. ruber* and *R. naevius*. Thus, the three most frequent hummingbird visitors of *P. nuda* had different foraging behaviors. In addition to hummingbirds, occasional visitors on *P. nuda* were hymenopterans and lepidopterans, notably *Bombus* spp., *Heliconius* spp. and *Trigona* spp., as observed previously by Castro and Araujo (2004).

Along the transect, hummingbird abundance and visitation rate were both found to fit a piecewise linear regression model better than a linear or quadratic model (Table 1). Hence, hummingbird abundance and visitation rate to *P. nuda* increased steeply toward the feeders at close distance, but showed a distance-related trend only up to a certain breakpoint. The piecewise linear regression indicated a breakpoint in hummingbird abundance at 74 m

(95 % CI 29 m,  $p = 0.003$ ; Fig. 2a) and for visitation rate at 125 m (95 % CI 35 m,  $p < 0.001$ ; Fig. 2b). We consider it unlikely that floral abundance has introduced biases related to the detected changes in hummingbird abundance and visitation rate along the transect. Notably, the floral abundance of *P. nuda* showed no distance-related trend away from the feeders ( $58.1 \pm 41.6$ ; Spearman’s  $r = -0.302$ ,  $p = 0.273$ ). Similarly, the variation in floral abundance of other hummingbird-visited plants was not related to the distance from the feeders ( $5.8 \pm 10.9$ ; Spearman’s  $r = -0.229$ ,  $p = 0.413$ ). Visitation rate was also not correlated with the averaged abundance of *P. nuda* flowers (Spearman’s  $r = 0.296$ ,  $p = 0.284$ ), nor with the abundance of other hummingbird-visited plant species (Spearman’s  $r = 0.109$ ,  $p = 0.694$ ). Instead, visitation rate was significantly positively associated with hummingbird abundance (Spearman’s  $r = 0.629$ ,  $p = 0.012$ ). The

**Table 1** Results from three different linear regression models testing the association between distance from the feeders and hummingbird abundance, visitation rate and pollen deposition, respectively

	<i>p</i> value	AIC	ΔAIC	<i>R</i> <sup>2</sup>	Adjusted <i>R</i> <sup>2</sup>
Hummingbird abundance					
Linear	0.028	82.369	22.418	0.321	0.269
Quadratic linear	0.002	74.958	15.007	0.637	0.577
Piecewise linear	<b>0.003</b>	<b>59.951</b>	<b>0</b>	<b>0.883</b>	<b>0.852</b>
Visitation rate					
Linear	0.008	67.104	26.361	0.434	0.391
Quadratic linear	0.003	62.923	22.18	0.625	0.563
Piecewise linear	<b>&lt;0.001</b>	<b>40.743</b>	<b>0</b>	<b>0.925</b>	<b>0.905</b>
Pollen deposition					
Linear	0.681	124.821	−0.257	0.013	−0.063
Quadratic linear	0.363	124.492	−0.586	0.155	0.015
Piecewise linear	0.818	125.078	0	0.231	0.021

Models with ΔAIC <2 are considered equally fit. Best-fit models are marked in bold

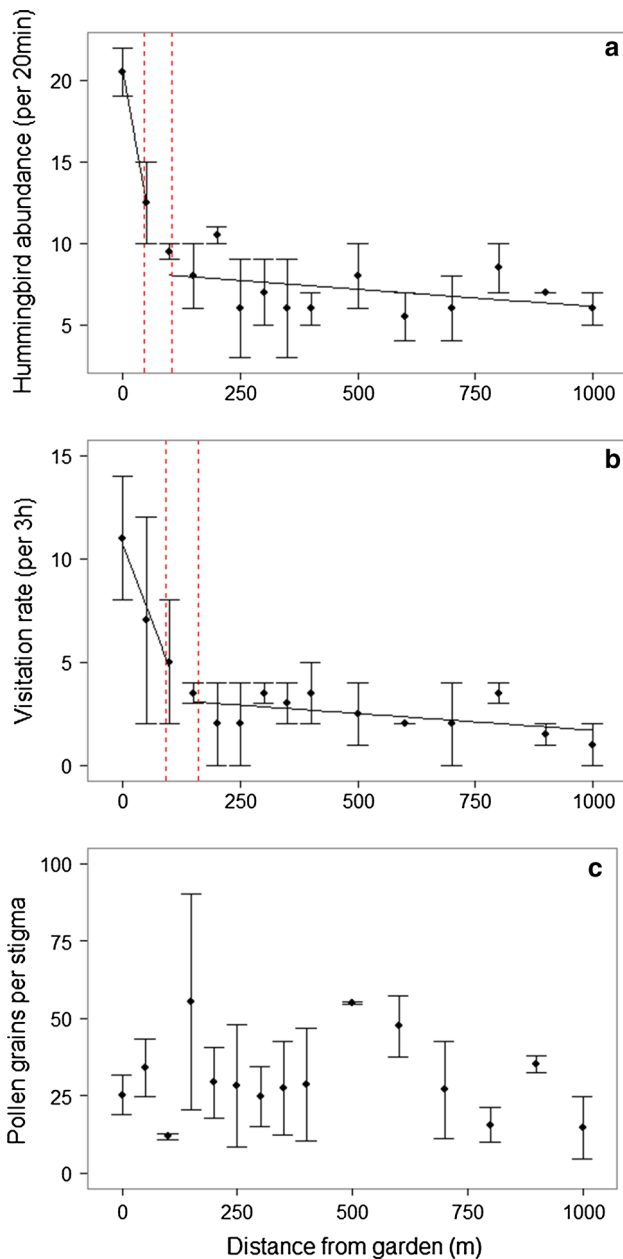
residuals from a model predicting visitation rate with hummingbird abundance along the transect did not change significantly with distance from the feeders, neither with a linear model ( $p = 0.208$ ), a quadratic ( $P = 0.381$ ), nor with a piecewise linear model ( $p = 0.818$ ). This indicates that individual hummingbird foraging rates on *P. nuda* remained similar throughout the transect. In contrast to hummingbird abundance and visitation rate, pollen deposition on stigmas was not related to distance in any of the three models (Fig. 2c; Table 1).

## Discussion

We have provided empirical evidence that the presence of artificial nectar feeders increased local hummingbird abundance and flower visitation rate to *P. nuda* to a distance of approximately 100 m from the feeders, but had no measurable effects beyond this distance (Fig. 2a, b). This pattern, however, was not reflected in pollen deposition on *P. nuda*, which showed no relationship to distance from the feeders, despite the higher visitation rates closer to the feeders (Fig. 2c). It is sometimes assumed that the frequency of interactions is a good indicator of pollinator importance (Vázquez et al. 2005). Since our results did not support this, we speculate that hummingbird visitation rate may not be a good proxy for the pollination of *P. nuda*, as also shown for other species (e.g., Watts et al. 2012; King et al. 2013). Irrespective of the exact explanation, flowers close to the feeders received at least ten pollen grains per flower, which was equivalent to the pollen deposition measured at the largest distance away from the feeders (Fig. 2c), and is potentially sufficient to ensure full pollination, as *P. nuda* only has two ovules (J Afonso, M do Carmo FW Amorim & VLG Brito, personal

communication). Therefore, we found no evidence that the presence of feeders negatively affected pollen deposition and plant reproductive fitness. When accounting for hummingbird abundance, residual visitation rate showed no distance-related trend, indicating that individual hummingbirds forage at similar rates on *P. nuda* throughout the transect. Thus, the primary effect of the feeders is to increase hummingbird abundance and thus visitation rates on *P. nuda* within a local environment of approximately 100 m around the feeders.

The results presented here support those from a previous study on the same topic (Brockmeyer and Schaefer 2012), but other studies documented contradictory results of reduced hummingbird visitation rate to flowers and smaller stigma pollen loads close to nectar feeders (Arizmendi et al. 2007; Avalos et al. 2012). In relation to Arizmendi et al. (2007), our experimental design differed substantially in respect to the amount of time the feeders have been present: 1 day in the case of Arizmendi et al. (2007) and 13 years in our case. When feeders have been present for more than a decade, the hummingbirds have had ample time to respond demographically, or simply to adjust the local distribution of individuals, to the extra amount of resources offered by the feeders. As an example, neither *A. versicolor*, *C. rubricauda* nor *H. cyanus* were initially observed around the feeders when they were set up in 2001; only after approximately 7 years of continuous feeding did these species start to appear (J d'Abronzio, personal communication). Eventually, as competition increases around the feeders, the surrounding flowers may represent an increasingly attractive resource. Thus, the apparent contradiction with Arizmendi et al. (2007) could be explained by an initial negative effect of feeder presence on the pollination of hummingbird-dependent plants, which gradually neutralized with time as hummingbirds adjusted



**Fig. 2** The association between distance from the feeders and **a** average hummingbird abundance; **b** average visitation rate; and **c** average pollen deposition. A piecewise linear regression is shown for hummingbird abundance and visitation rate with estimated breakpoints of  $74 \pm 29$  m (abundance) and  $125 \pm 35$  m (visitation rate). The dashed lines are 95 % confidence intervals of the breakpoints. Pollen deposition was unrelated to distance from the feeders. Standard errors are shown for each point measurement ( $n = 2$ ). Feeders are situated approx. 20 m from the 0 m point of the transect (see “Methods” section)

demographically to the new resource availability. Avalos et al. (2012) used a different approach to quantify potential effects on the pollination service provided by hummingbirds: by capturing birds with mist nets across 2 years, they found lower pollen loads on hummingbirds near feeders

compared to 3 km away. This could possibly explain why pollen deposition does not increase with visitation frequency and hummingbird abundance close to the feeders. It is also worth noting that pollen deposition does not necessarily imply pollination. In this regard, one could have used other measures such as number of pollen tubes growing down the styles or seed set, which are both more direct measures of plant reproductive fitness. Nevertheless, these are also affected by other factors, such as pollen compatibility for pollen tube growth and resource limitation of the maternal plant during seed set. Pollen deposition thus gives valid, but not exhaustive, information about the pollination services provided by hummingbirds.

Considering species composition, *P. ruber* was the only hummingbird entirely absent from the feeders and at point 0 m just outside the garden. This is surprising, considering the fact that it was the second most abundant species along the transect (Fig. 1b) and is one of the most common hummingbirds found in the region, including human-altered secondary forest habitats (Maruyama et al. 2015), which may be avoided by some species (Wethington and Finley 2009). Knowing that hummingbirds commonly show aggressive behavior around resource-rich patches and hierarchical dominance relate to body size (Justino et al. 2012), one explanation could be the relatively small size of *P. ruber*, which could make it more prone to competitive exclusion from the feeders by larger territorial or even larger traplining hummingbirds, such as *T. glaucopsis*. We note that differences in sugar concentration between sugar water in the feeders and nectar from flowers in some cases may explain the absence of hermit hummingbirds at feeders, as hermit hummingbirds often favor flowers with high nectar concentration (Stiles and Freeman 1993). We think the low sugar concentration is an unlikely cause for the absence of *P. nuda* for two reasons. First, one of the most common hummingbirds recorded at the feeders is a large hermit, *R. naevius*. Second, sugar concentration in the feeders exceeds the concentration in *P. nuda* nectar (Castro and Araujo 2004), and both *P. ruber* and *R. naevius* as well as other hermit hummingbirds are commonly observed visiting this plant in the region (Maruyama et al. 2015). That differences in foraging behavior, e.g., territorial vs. trapliner, might account for the absence of *P. ruber* seems also unlikely, as the most common hummingbird observed at the feeder was *R. naevius* (Fig. 1a, b), a large hummingbird that is very common in the region and has distinctive traplining behavior when visiting flowers (Sazima et al. 1995; Maruyama et al. 2015).

All other nine species of hummingbirds responded to the presence of feeders by showing higher abundance close to the feeders (Fig. 1a, b). Therefore we suggest that the distance related trend in hummingbird abundance is not associated with a corresponding change in

hummingbird richness, as one could hypothesize (Fig. 1b), but rather reflects infrequent recordings of hummingbird individuals beyond the mentioned 100 m from the feeders. In other words, relative hummingbird abundance increases close to the feeders, whereas richness seems less affected, perhaps with the exception of *P. ruber* being absent at the feeders.

Hummingbirds are important pollinators in Neotropical ecosystems, and it is therefore relevant to consider their role from an ecosystem perspective (Nicolson and Fleming 2003). In this regard, our results indicate that applying supplementary feeding does not necessarily disrupt hummingbird pollination services. This suggestion, however, needs empirical support from more hummingbird-pollinated plant species. Notably, it would be important to test an array of plant species with different degrees of specialization to hummingbird pollination, including plants specialized exclusively on long-billed hummingbird species. Additionally, future studies should aim at also evaluating the effect on pollen tube growth and seed set. Finally, it would be relevant to investigate the response in hummingbird foraging behavior to the inter-annual variation in floral abundance and test whether pollinators would be less attracted to feeders in years with high floral abundance (Inouye et al. 1991; McCaffrey and Wethington 2008). In the light of anthropogenic changes in climate and land use, which may affect pollinator assemblages and therefore disrupt pollination services (Memmott et al. 2007; Ollerton et al. 2014), knowledge on the effect of seemingly “trivial” human activity such as animal attraction through artificial feeders becomes increasingly relevant (Galbraith et al. 2015). This applies not only to hummingbirds, but also to other animal pollinators such as mammals and insects. We therefore hope this study may inspire further research into the effect of nectar-feeders on hummingbirds and other animal pollinators and their food-plants.

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