



Do artificial nectar feeders affect bat–plant interactions in an Ecuadorian cloud forest?

Rossana Maguina¹ , and Nathan Muchhala

Department of Biology, University of Missouri–St. Louis, One University Blvd., PO Box 211401 UMSL R223, St. Louis, MO 63121-4400, U.S.A.

ABSTRACT

Plant–pollinator interactions are critical to ecosystems. However, when artificial nectar feeders are available in an area, they could draw pollinators away from plants. We tested the effects of artificial nectar feeders in an Ecuadorian cloud forest on four aspects of bat–plant interactions: (1) bat relative abundance; (2) bat pollen loads; (3) flower visitation rates, and (4) breeding success of a bat-pollinated species (*Burmeistera glabrata*). We divided the study site into areas close to (~30 m) and far from (~500 m) three different feeder sites. At each distance, we captured nectar bats (*Anoura caudifer*, *Anoura cultrata*, and *Lonchophylla robusta*) to estimate their relative abundance and to collect pollen from fur and fecal samples. We also videotaped flowers to estimate bat visitation rates and recorded different breeding success variables of *B. glabrata*. We found that areas close to feeders have higher relative bat abundance by a factor of 40. In spite of this, the presence of feeders did not affect bat pollen loads, nor the flower visitation rates and breeding success of *B. glabrata*. Interestingly, there were differences in pollen loads between the three bat species, in that *L. robusta* individuals rarely carried pollen and were only captured near feeders.

Abstract in Spanish is available with online material.

Key words: *Burmeistera glabrata*; flower visitation rate; hummingbird feeders; nectar bats; plant-breeding success; pollen.

IN MANY SOUTH AMERICAN COUNTRIES, THERE IS A GROWING MARKET FOR ECOTOURISM, and bird watching is a very popular activity (Brockmeyer & Schaefer 2012). Hummingbirds are particularly appreciated, and to allow prolonged observation of them, there has been increasing use of artificial nectar feeders in many ecologies, including nature reserves that protect important remnants of endangered ecosystems (Brockmeyer & Schaefer 2012). Since feeders typically remain functional during the night, they not only attract hummingbirds but also attract bats (Hinman 2003; pers. obs., Video S1).

When feeders are available in an area, they could draw pollinators away from plants with their enormous and predictable quantities of artificial nectar (Arizmendi *et al.* 2007, Brockmeyer & Schaefer 2012). Plant–pollinator interactions are critical to ecosystems because they determine the reproductive success of animal-pollinated plant species, and more generally, they can contribute to speciation in plants and to the maintenance of biodiversity (Fontaine *et al.* 2006, Gegear & Burns 2007, Fleming *et al.* 2009). To implement optimal management decisions for the conservation of these interactions (Ghazoul 2005), it is necessary to know how feeders affect them (Avalos *et al.* 2012, Brockmeyer & Schaefer 2012).

Most of our knowledge about the effects of feeders on plant–animal interactions is derived from studies of plant–hummingbird interactions, and this literature shows contrasting results. For instance, Brockmeyer and Schaefer (2012) found that there are no overall effects of feeders on hummingbird visitation to

nearby flowers, while Sonne *et al.* (2016) found feeders increased hummingbird abundance and visitation rates to flowers of *Psychotria nuda* within a 100-m radius. Other studies concluded that feeders attract hummingbirds across considerable distances (3-km radius), drawing them away from flowers and decreasing visitation rates in this area (Inouye *et al.* 1991, Arizmendi *et al.* 2007, Avalos *et al.* 2012). Arizmendi *et al.* (2007) also found a significant decrease of plant reproductive success of the native *Salvia fulgens* in the areas close to feeders. The only study to examine pollen loads found that hummingbirds captured close to feeders carried very low pollen abundance and diversity on their bodies (Avalos *et al.* 2012). In the case of bat–plant interactions, the impact of feeders has been poorly studied. In the only study we are aware of on the topic, Hinman (2003) found that feeders are a major source of energy for nectar bats in southeastern Arizona and suggested that this may affect visitation to flowers in the area.

This is the first study to test the effects of feeders on bat–plant interactions. We experimentally tested these effects on four aspects of bat–plant interactions in a cloud forest of eastern Ecuador: (1) bat relative abundance; (2) pollen loads carried by bats; (3) visitation rates to bat-pollinated plants; and (4) breeding success of these plants. We expect that bat relative abundance will be higher in areas closer to the feeders, which could lead to either an increase or decrease in pollination of nearby flowers. Bats could prefer feeding from feeders rather than nearby flowers, causing lower visitation rate, pollen loads, and plant breeding success. Alternatively, bats could feed from feeders and nearby flowers, and the higher number of bats would thus increase flower visitation rates and plant breeding success in those areas, although pollen loads per bat would likely still decrease.

Received 20 October 2016; revision accepted 30 March 2017.

¹Corresponding author; e-mail: nrmaguina@gmail.com

METHODS

STUDY SITE AND FOCAL SPECIES.—We conducted this study in cloud forests of the eastern Ecuadorian Andes, in the private protected area of Wildsumaco Wildlife Sanctuary (0°40.3' S, 77°35.5' W). The area is located in the Napo province at elevations between 1310 and 1480 m, adjacent to the Sumaco-Napo Galeras National Park, and harbors a wide diversity of flora and fauna, including 22 bat species (Coloma-Santos 2007). Wildsumaco maintains three areas with hummingbird feeders: one near the tourist lodge, one near the biological research station, and one along a trail. Each feeder area contained eight to ten feeders that lodge employees fill every morning with a 1:4 sugar-water solution. At night, bats feed on remaining nectar (pers. obs., Video S1). All feeder sites were similar in terms of type of surrounding vegetation and distance to trails and roads, except that the exposure to artificial light at night was higher in the feeder site closer to the tourist lodge, and the vegetative cover was higher in the feeder site closer to the biological station.

We focused our work on the nectarivorous bats species *Anoura candifer*, *A. cultrata*, and *Lonchophylla robusta* (Phyllostomidae), previously recorded in the area (Lee *et al.* 2010, Burneo & Tirira 2014). Our focal plant species, *Burmeistera glabrata* (Campanulaceae), is an understory free-standing or hemi-epiphytic subshrub (Jeppesen 1981). Species of *Burmeistera* are primarily adapted to pollination by bats (Muchhala 2006), and *B. glabrata* presents floral traits corresponding to the chiropterophilous pollination syndrome (von Helversen 1993): the flowers are green and emit odor, they are well exposed on long pedicels, anthesis is nocturnal (lasting between 4 and 6 days), and the individuals remain in flower throughout the year with one to four flowers open at a time. Previous videos taken by one of the authors (N.M) recording pollinators visiting *B. glabrata*'s flowers confirmed that bats are the only effective pollinators of this species. We chose this species as our focal plant because it is very abundant and easy to find at the study site.

EXPERIMENTAL DESIGN.—To measure the effect of feeders on bat-plant interactions, we divided each of the three nectar feeder areas into one region within a 30-m radius of the feeders and a second, paired region approximately ~500 m away, for a total of six study areas. Fieldwork was conducted during June–July 2015 and January–February 2016. Each night, we worked simultaneously in a 'closer' feeder area and its paired 'farther' area to avoid any temporal biases in sampling. We employed four methods.

Bat relative abundance.—We captured bats in each distance area using four mist nets (mist net sizes: height 3 or 2.5 m; length 2, 6, 9, or 12 m). We set up the nets near bat-pollinated plant species (in front of flowers or surrounding the whole plant) or across possible flight paths, in similar areas in close and far distance areas, for 15 nights and 19 nights, respectively. We opened the mist nets from 1 hour after dusk to midnight (19:00–24:00 h). By waiting for an hour after dusk, we hoped to allow bats to feed before we caught them, and thus increase chances of

obtaining pollen in fur and fecal samples. We calculated bat relative abundance as the number of bats captured per mist net per hour.

Pollen loads.—We collected pollen from the fur of captured bats by touching transparent adhesive tape against three different bat body regions: head, belly, and inner wing patagium. We placed the tape on a microscope slide for later analysis in the laboratory. Bats were then placed in cloth bags for 2 hours to collect fecal samples, which were preserved in 70 percent ethanol. In the laboratory, we mounted fecal samples on microscope slides and covered them with adhesive tape for analysis. We inspected the fur and fecal samples using a light microscope (SWIFT Microscope World, Carlsbad, California, U.S.A.), conducting a scanning of the tape at 100×, and switching to 400× to identify and photograph the pollen grains. For each sample, we recorded the presence or absence of pollen (pollen frequency). When present, we estimated the pollen abundance as rare (<=100 pollen grains) or abundant (>100 pollen grains) and counted the number of types of pollen (pollen diversity). We identified the pollen using our own pollen reference collection from the area and the pollen atlas of Roubik and Moreno (1991).

Flower visitation rates.—To obtain *B. glabrata* flower visitation rates, we videotaped flowers using a SONY camcorder with the Night Vision function (SONY Corporation of America, New York, U.S.A.) from 18:00 to 23:00 h. We did not videotape flowers the same day that we mist-netted bats to avoid affecting the results. For each flower videotaped, we recorded the number of open flowers on the focal individual and on all individuals within a 5-m radius to estimate local floral patch size. In addition, we measured the relative abundance of *B. glabrata* per distance area using four randomly selected circular plots (5-m radius).

Plant breeding success.—We measured the breeding success of *B. glabrata* using three different approaches. First, we selected and marked between five and ten individuals of similar sizes in each distance area, and we counted the number of fruits present on each individual to estimate the average number of fruits produced per individual in each distance area. Second, we collected between one and seven fruits per individual and counted the number of seeds produced per fruit. Finally, after flowers fell, we tracked the remaining hypanthia (which eventually form the fruits) to track fruit abortion rates. We counted and marked the hypanthia present on each individual, and after five days, we recounted the marked hypanthia that remained. That same day we counted and marked new hypanthia present, and after five more days, we recounted the new marked hypanthia.

STATISTICAL TESTS.—To assess whether bat relative abundance, flower visitation rate, and breeding success variables differ between close and far-distance areas, we applied a linear mixed-effects model (LMM) using distance area as a fixed effect and feeder site as a random effect. We transformed the nonparametric data (bat relative abundance, flower visitation rate, percentage of fallen hypanthia) using adjusted ranks (Leys & Schumann

2010). To compare *B. glabrata* relative abundance, we used a *t*-test, and to compare pollen load variables, we used chi-square and Fisher test for normally distributed data and Mann–Whitney *U* and Kruskal–Wallis tests for nonparametric data. Finally, we used a Spearman’s correlation to determine whether flower visitation rate was related to the local floral patch size. All statistical analyses were performed with R 3.2.2 (The R Foundation, Vienna, Austria).

RESULTS

BAT RELATIVE ABUNDANCE.—We captured 91 bats in areas close to feeders and eight in farther areas, including the species *A. caudifer*, *A. cultrata*, and *L. robusta*. However, *A. cultrata* and *L. robusta* were only captured in closer areas. The LMM showed that bat abundance was significantly higher in closer (0.9 ± 1.7 bats per mist-net/h) than in farther areas (0.02 ± 0.07 bats per mist-net/h) from feeders ($P < 0.01$, Table 1). In addition, we repeated the LMM test for only *A. caudifer*, which also showed significantly higher abundance in closer (0.5 ± 1.2 bats per mist-net/h) than in farther (0.02 ± 0.07 bats per mist-net/h) areas ($P < 0.01$, Table 1).

POLLEN LOADS.—We collected pollen samples from fur for all 99 bats that we captured, and 26 additional fecal samples. Pollen from *Marigravia* sp. (80.4%) and *Burmeistera glabrata* (77.3%) were most frequently recorded, followed by bromeliads, *Ocroma pyramidale*, and *Abutilon* spp. (Table S1). There was no significant difference between the closer and farther areas in terms of pollen frequency: pollen was present on 89 (97.8%) of the bats in closer areas and eight (100%) of the bats in farther areas (chi-square, $\chi^2 = 0.6$, $P = 0.41$). Farther areas had a significantly greater proportion of samples categorized as having abundant pollen (chi-square, $\chi^2 = 41.8$, $P < 0.01$, Figure S1), with eight (100%) versus 58 (63.73%), as well as a significantly higher pollen diversity, with 4.3 ± 1.6 pollen types/sample versus 3.3 ± 1.2 pollen types/sample (Mann–Whitney *U*-test, $U = 193.5$, $P = 0.02$, Fig. 1).

TABLE 1. Bat relative abundance in areas close to (<30 m) and farther from (>500 m) the feeders. The mean relative abundance per bat species is a measure of the number of bats captured per mist net per hour.

Bat species	Close areas		Far areas	
	Individuals captured	Mean relative abundance ^a	Individuals captured	Mean relative abundance ^a
<i>Anoura caudifer</i>	36	0.5 ± 1.1^b	8	0.02 ± 0.07^b
<i>Anoura cultrata</i>	4	0.07 ± 0.3	0	0
<i>Lonchophylla robusta</i>	51	0.43 ± 0.7	0	0
Total	91	0.907 ± 1.7	8	0.023 ± 0.07

^a± SE. LMM, all bat species: Estimate (SE) = 26.84 (5.3), $df = 107$, $t = 5.01$, $P < 0.01$, only *A. caudifer* samples; ^bEstimate (SE) = 29.62 (5.3), $df = 107$, $t = 5.01$, $P < 0.01$.

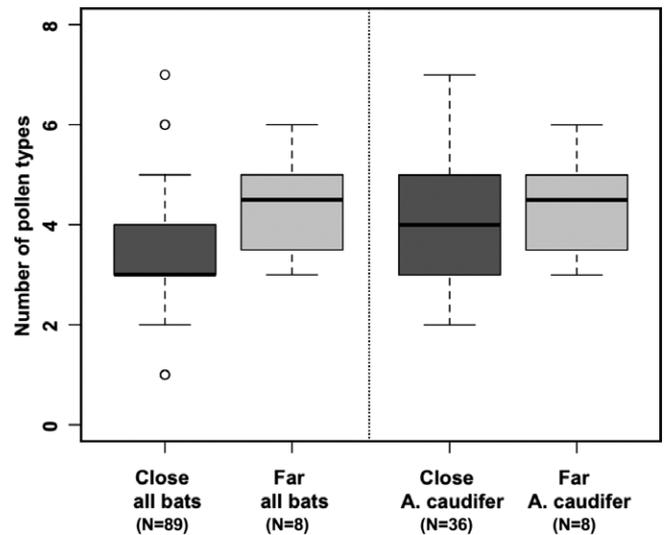


FIGURE 1. Pollen diversity in areas close to and far from feeders based on the full sample set (including all three bat species), and the sample set with only *A. caudifer*.

However, because the species *A. cultrata* and *L. robusta* were captured only in closer areas, we repeated these tests for only the *A. caudifer* captured in the two distances. This new sample set includes 36 in closer and eight in farther areas. In this case, there was no significant difference between any of the variables (pollen frequency and abundance, Fisher’s exact *t*-test, $P = 1.0$, Figure S1; pollen diversity, Mann–Whitney *U*-test, $U = 133$, $P = 0.73$, Fig. 1). We also tested whether frequency, abundance, and diversity of pollen loads differ between the three bat species caught in closer areas to feeders. Results showed a significant difference among species for abundance (chi-square test, $\chi^2 = 160.3$, $P < 0.01$, Fig. 2) and diversity of pollen loads (Kruskal–Wallis test, $\chi^2 = 29.6$, $df = 2$, $P < 0.01$, Fig. 3): *A. caudifer* and *A. cultrata* had higher pollen abundance than *L. robusta*, and *A. caudifer* had the highest pollen diversity among the three species. Finally, *B. glabrata* pollen frequency was significantly higher in farther than closer areas (chi-square, full data set, $\chi^2 = 25.9$, $P < 0.01$ and only *A. caudifer* samples, $\chi^2 = 3.8$, $P = 0.05$).

FLOWER VISITATION RATE.—We videotaped 30 *B. glabrata* flowers in areas closer to feeders and 44 in farther areas. The LMM showed that flower visitation rate was not significantly different between closer (0.276 ± 0.4 visits per flower/h) and farther (0.313 ± 0.53 visits per flower/h) areas ($df = 70$, $P = 0.32$, Table 2). The relative abundance of *B. glabrata* was also not significantly different between closer (2.58 ± 2.23 individuals) and farther (2.33 ± 1.87 individuals) areas (Fisher’s exact *t*-test, $P = 0.77$). The flower visitation rate was not related to the local floral patch size, including the number of open flowers on the focal plant for either closer ($S = 917.1$, $P = 0.68$) or farther areas ($S = 5621.2$, $P = 0.1$), or the number of nearby open flowers (within a 5-m radius; $S = 948$, $P = 0.73$; farther areas $S = 8396.5$, $P = 0.84$).

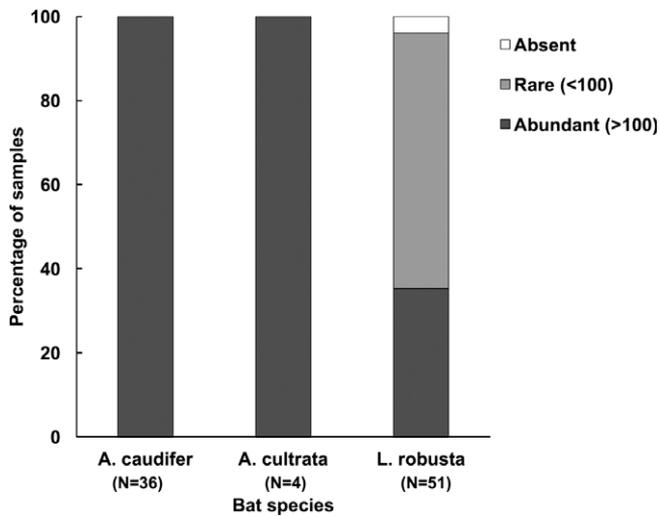


FIGURE 2. Percentage of samples with each category of pollen load size for the three bat species in areas close to feeders. 'Absent' corresponds to no pollen, 'Rare' to fewer than 100 grains, and 'Abundant' to more than 100 grains.

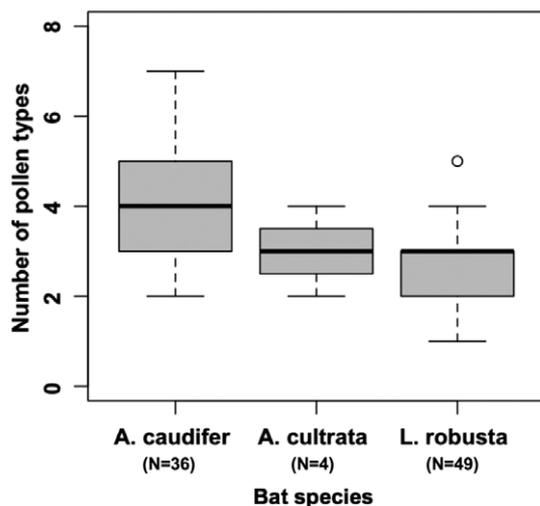


FIGURE 3. Pollen diversity on the three bat species in areas close to feeders.

PLANT-BREEDING SUCCESS.—We took measurements of plant-breeding success variables from 34 and 47 plant individuals in closer and farther areas from feeders, respectively (Table 2). The LMM showed no significant differences between distance areas (close to or far from feeders) for any of the four plant-breeding success variables, including number of fruits, number of seeds, percentage of fallen hypanthia, and seed set per flower (Table 2). Seed set per flower was calculated multiplying the average number of seeds per fruit per individual by its proportion of remaining hypanthia and marked hypanthia in each distance area.

DISCUSSION

This study found a large increase in nectar bat abundance close to hummingbird feeders. Despite this, there was no apparent

effect of feeders on pollen loads carried by bats, flower visitation rates, or the breeding success of the bat-pollinated species *B. glabrata*. The only exception was the frequency of *B. glabrata* pollen carried by the bats, which was higher in the areas farther from feeders. We also found differences in pollen loads between the three species of bats, with *A. caudifer* carrying more than *A. cultrata*, and both carrying more than *L. robusta*. Some caveats are warranted in interpreting our results. Specifically, we note that bat sample sizes were low in our nonfeeder areas, that the study only encompassed a portion of the year, and that only three feeder versus nonfeeder areas were compared. However, the data are consistent across these three replicates in suggesting that feeders increase bat abundance without negatively affecting nearby pollination success, a particularly important and encouraging conclusion given its conservation implications.

BAT RELATIVE ABUNDANCE.—We found a higher relative abundance of bats in areas closer to the feeders by a factor of 40. Similarly, when we considered only the bat species captured in both distance areas (*A. caudifer*), we found a higher abundance of this species closer to feeders by a factor of 24. These results agree with previous studies that found a higher abundance of hummingbirds in areas near feeders (Sonne *et al.* 2016), and confirm that feeders will similarly attract and affect the local distribution of hummingbirds and bats. Interestingly, we found that the species *L. robusta* and *A. cultrata* were only captured in areas closer to the feeders. For *A. cultrata*, this discrepancy may be simply an artifact of low capture rates (we only captured 4 in total), given that we have caught *A. cultrata* in forests away from feeders in Wildsumaco previously, particularly with nets located close to *Marcgravia* flowers (pers. obs). However, for *L. robusta*, previous captures in the area were also equally unsuccessful at capturing them away from feeders (Lee *et al.* 2008 and pers. obs; we captured only a single individual in eight netting nights in July 2015).

Wildsumaco's altitude (~1400 m) exceeds the previously known upper elevation limit of *L. robusta* (800 m, Dávalos *et al.* 2015), unlike that of the two species of *Anoura*, whose distributions reach up to 2880 m (*A. caudifer*, Solari 2016) and 2600 m (*A. cultrata*, Molinari & Mantilla-Meluk 2016). Tschapka (2004) observed that *L. robusta* individuals typically began to be captured in mist nets 1 hour after other nectar bat species and that they were captured in particularly large numbers next to a plant that produced copious amounts of high-energy nectar, suggesting a foraging strategy involving long flights after sunset to distant feeding areas with predictable and rich resources. Because we opened mist nets an hour after dusk, we cannot make a similar comparison between capture times; however, when we videotaped bat's activity at one feeder site, we noted that *L. robusta* arrived 30 min after *A. caudifer*. This, along with the fact that we only captured *L. robusta* individuals next to feeders and that they carried little pollen, suggests that they are foraging similar to the *L. robusta* observed by Tschapka (2004) in Costa Rica. Perhaps, they roost at intermediate elevations and travel up to Wildsumaco to exploit the large amounts of artificial nectar the feeders provide. Their larger body size (compared to *A. caudifer*) would allow

TABLE 2. Effects of feeders on reproductive success of *Burmeistera glabrata*, in terms of flower visitation rates and fruit and seed production.

Variables	N	Sample unit	Mean ± SE	Fixed effect				Random effect (SD)	
				Estimate (SE)	df	t value	P value	Intercept	Residual
<i>Flowers visitation rate</i> ^a									
Close areas	14	Flower	0.276 ± 0.4 visits/hr	−4.95 (4.9)	70	−1	0.32	6.46	20.7
Far areas	12		0.313 ± 0.53 visits/h						
<i>Average number of fruits</i> ^b									
Close areas	23	Plant individual	16.78 ± 16.8 fruits	−0.45 (0.3)	47	−1.62	0.11	2.96 × 10 ^{−5}	0.98
Far areas	28		7.67 ± 6.09 fruits						
<i>Average number of seeds</i> ^a									
Close areas	25	Fruit	1166.22 ± 374.01 seeds	29.77 (80.4)	54	0.37	0.71	141.43	292.17
Far areas	33		1192.87 ± 323.04 seeds						
<i>Percentage of fallen hypanthia (%ofh)</i> ^b									
Close areas	16	Plant individual	35.86 ± 33.18%fh	−0.19 (4)	39	−0.04	0.96	15.35	26.2
Far areas	27		48.66 ± 36.99%fh						
<i>Set of seeds per flower</i> ^b									
Close areas	13	Flower	832.83 ± 433.82 seeds/flower	−194.79 (166.5)	28	−1.16	0.25	0.02	462.59
Far areas	19		638.03 ± 480.82 seeds/flower						

^aSampled in 2015 and 2016, ^bSampled only in 2016, SE = standard error, SD = standard deviation.

them to fly relatively long distances seeking food resources (Von Helversen & Winter 2005). Thus, feeders may differentially affect nectar bat species depending on their foraging behavior, attracting them from either local forests or long distances.

POLLEN LOADS.—We did not find a consistent effect of feeders on pollen loads carried by the species *A. caudifer* in Wildsumaco. Results using the full sample set (with all three species pooled) showed higher abundance and diversity of pollen in nectar bats captured in farther areas, while results including only *A. caudifer* showed similar values of pollen frequency, abundance, and diversity in both distance areas. Thus, the low pollen loads carried by *L. robusta* appear to be driving the pattern in the full sample set. We suspect that this reflects differences in feeding behavior among bat species in terms of flower preferences or feeding activity patterns. It is worth noting that feeders can provide large amounts of carbohydrates in the nectar but do not provide protein, which nectar bats typically obtain mainly from pollen groomed from their fur after flower visits (Herrera *et al.* 1998). Thus, feeders might be expected to have less of an impact on bat–flower interactions than on hummingbird–flower interactions, given that hummingbirds do not ingest pollen. In fact, 89 of the 91 bats caught near the feeders were carrying at least some pollen, demonstrating that they are still visiting flowers.

The pollen frequency of *B. glabrata* was higher in farther than closer areas in both analyses; however, our other results (below) suggest that this does not affect the breeding success of this species. Ours is the first study to statistically compare pollen loads between pollinators flying close to and far from feeders, although Avalos *et al.* (2012) anecdotally noted that

hummingbirds captured close to feeders carried little or no pollen on their bodies (low frequency and abundance) and the majority of those with pollen had only one type (low diversity).

FLOWER VISITATION RATE.—Videotaping shows that there was no effect of feeders on bat visitation rates to *B. glabrata* flowers. Our results concur with previous studies that found no significant differences in hummingbird visitation rates to flowers located at different distances to feeders (Brockmeyer & Schaefer 2012), but contrast with others that found an increase (Sonne *et al.* 2016) or a decrease (Arizmendi *et al.* 2007) closer to the feeders. Sonne *et al.* (2016) stated that the increase in flower visitation rate is due to higher hummingbird abundance in the area; in our case, although we found higher bat abundance, we did not find a higher visitation rate near feeders. This could be due to unknown behavioral differences among these two pollinator guilds or to differences in sugar concentration among hummingbird and bat pollinated plant species (Perret *et al.* 2001) which, in the case of *B. glabrata*, could make it be less attractive than the feeders. Regarding the study of Arizmendi *et al.* (2007), they applied a different methodology that could have led to results that contrast with our study (and that of Sonne *et al.* 2016). They designed an experiment with the control and treatment areas containing ten individuals of hummingbird-pollinated plants and introduced two feeders into the treatment areas. The sudden, novel presence of feeders would likely attract many hummingbirds, drawing them away from farther areas and increasing visitation rates in closer areas (Arizmendi *et al.* 2007, Sonne *et al.* 2016). Our experimental design used feeders that had been in their current locations for at least 7 yr, allowing time for the pollinators to adjust their distributions accordingly.

PLANT-BREEDING SUCCESS.—We did not find an effect of feeders on the reproductive success of *B. glabrata*. There were similar values for number of fruits, number of seeds, percentage of fallen hypanthia, and seed set per flower in areas close to and farther from feeders. Our results are consistent with findings of Sonne *et al.* (2016), who did not find differences in the amount of pollen deposited by hummingbirds on flower stigmas along a distance gradient from feeders. Although Arizmendi *et al.* (2007) used a different experimental design (as discussed above), it is worth noting that they obtained different breeding success results for each of the plant species they worked with. Seed production of *Salvia fulgens* was lower in individuals exposed to the feeders, whereas seed production of *S. mexicana* was similar between exposed and nonexposed individuals (Arizmendi *et al.* 2007), suggesting that effects may be species specific. In our study, we did not find a negative effect of feeders on the breeding success of *B. glabrata*; however, we note that this is the most abundant bat-pollinated species in the area; feeders might be expected to have a larger negative impact on rare plant species (McCaffrey & Wethington 2008).

We conclude that feeders are highly attractive to bats, increasing their abundance close to the feeders by a factor of 40. Despite this increase in abundance, the presence of feeders do not affect pollen loads carried by bats, flower visitation rates by bats, or breeding success of the bat-pollinated species *B. glabrata*. We also found differences in pollen loads between the three species of bats captured close to the feeders, with *A. caudifer* carrying more pollen than *A. cultrata*, and both carrying more than *L. robusta*, suggesting that there might be differences in feeding behavior among bat species in terms of flower preferences or feeding activity patterns. This is the first study to test the effects of feeders on bat–plant interactions. While results are encouraging, in that bats visiting feeders still carry pollen and pollination did not suffer near feeders, we suggest caution in generalizing results until further studies have been made in different habitats and with different species of nectar bats.

ACKNOWLEDGMENTS

We are grateful to Stephanita Mafla-Mills, María Fernanda Solorzano, Miluska Ramos, and Jorge Carrera for assistance with fieldwork; and Sophia Phillips, Sarah Kelley, Randy Beltz, Alexis Ramos, Ruth Abraha, and Ari Zakroff for assistance with laboratory work at the University of Missouri–St. Louis. We thank Wildsumaco Wildlife Sanctuary, Santiago Burneo, and Andrea Vallejo from Pontificia Universidad Católica del Ecuador for helping with the logistics in Quito; Theodore Fleming and two anonymous reviewers for comments on the manuscript; the community of Pacto Sumaco and 10 de Agosto and the forest rangers of the Sumaco Napo Galeras National Park for their hospitality and interest in our research. The University of Missouri–St. Louis Institutional Animal Care and Use Committee (IACUC) authorized the use of live animals under the protocol 732692-2. The Ministerio del Ambiente de Ecuador granted permission through the scientific permits 07-15-IC-FAU-DPAN/MA and 05-16-IC-FAU-DPAN/MA. This study was supported by the

Whitney R. Harris World Ecology Center at the University of Missouri–St. Louis.

DATA AVAILABILITY

Data available from the Dryad Repository: <http://dx.doi.org/10.5061/dryad.007s8> (Maguiña & Muchhala 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Plant species/genus/family recorded per bat individual based on pollen identification.*

FIGURE S1. Percentage of samples with abundant and not-abundant pollen based on the full sample set (including all three bat species) and the sample set with only *A. caudifer*.

VIDEO S1. Bats visiting feeder located next to the lodge area of Wildsumaco. File: Bats visiting feeder.mp4

LITERATURE CITED

- ARIZMENDI, M., M. CONSTANZA, J. LOURDES, F. IVONNE, AND L. EDGAR. 2007. Effect of the presence of nectar feeders on the breeding success of *Salvia mexicana* and *Salvia fulgens* in a suburban park near México City. *Biol. Cons.* 136: 155–158.
- AVALOS, G., A. SOTO, AND W. ALFARO. 2012. Effect of artificial feeders on pollen loads of the hummingbirds of Cerro de La Muerte, Costa Rica. *Rev. Biol. Trop.* 60: 65–73.
- BROCKMEYER, T., AND H. M. SCHAEFER. 2012. Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds? *Basic Appl. Ecol.* 13: 294–300.
- BURNEO, S. F., AND D. G. TIRIRA. 2014. Murciélagos del Ecuador: Un análisis de sus patrones de riqueza, distribución y aspectos de conservación. *Therya* 5: 197–228.
- COLOMA-SANTOS, A. 2007. Parque nacional sumaco napo-galeras. In *ECOLAP and MAE (Eds.). Guía del patrimonio de áreas naturales protegidas del Ecuador*, pp. 219–224. ECOFUND, FAN, DarwinNet e IGM, Quito, Ecuador.
- DÁVALOS, L., H. MANTILLA, C. MEDINA, J. PINEDA, AND B. RODRIGUEZ. 2015. *Lonchophylla robusta*. The IUCN Red List of Threatened Species 2015: e.T12268A22038399. <https://doi.org/10.2305/iucn.uk.2015-4.rlts.t12268a22038399.en>. Downloaded on 13 September 2016.
- FLEMING, T. H., C. GEISELMAN, AND J. KRESS. 2009. The evolution of bat pollination: A phylogenetic perspective. *Ann. Bot.* mcp197.
- FONTAINE, C., I. DAJOZ, J. MERIGUET, AND M. LOREAU. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol.* 4: 129–135.
- GEGEAR, R. J., AND J. G. BURNS. 2007. The birds, the bees, and the virtual flowers: Can pollinator behavior drive ecological speciation in flowering plants? *Am. Nat.* 170: 551–566.
- GHAZOU, J. 2005. Buzziness as usual? Questioning the global pollination crisis. *Tree* 20: 367–373.
- VON HELVERSEN, O. 1993. Adaptations of flowers to the pollination by glosophagine bats. In W. Barthlor, C. M. Naumann, K. Schmidt-Loske, and K.-L. Schuchmann (Eds.). *Plant-animal interactions in tropical environments*, pp. 41–59. Museum Alexander Koenig, Bonn.
- HERRERA, M., L. GERARDO, AND C. MARTÍNEZ DEL RÍO. 1998. Pollen digestion by New World bats: Effects of processing time and feeding habits. *Ecology* 79: 2828–2838.

- HINMAN, K. E. 2003. The nature of the mutualism between *Agave palmeri* and its bat pollinators (*Leptonycteris curasoae* and *Choeronycteris mexicana*) in south-eastern Arizona (PhD Dissertation). State University of New York.
- INOUE, D. W., W. A. CALDER, AND N. M. WASER. 1991. The effect of floral abundance on feeder censuses of hummingbird populations. *Condor* 93: 279–285.
- JEPPESEN, S. 1981. Lobeliaceae. In G. Harling, and B. Sparre (Eds.). *Flora of Ecuador*, No. 14, pp. 9–170. Swedish Natural Science Research Council, Stockholm, Sweden.
- LEE JR, T. E., BURNEQ, S. F., COCHRAN, T. J., & CHAVEZ, D. 2010. Small mammals of Santa Rosa, southwestern Imbabura Province, Ecuador.
- LEYS, C., AND S. SCHUMANN. 2010. A nonparametric method to analyze interactions: The adjusted rank transform test. *J. Exp. Soc. Psychol.* 46: 684–688. <https://doi.org/10.1016/j.jesp.2010.02.007>.
- MAGUIÑA, R., AND N. MUCHHALA. 2017. Data from: Do artificial nectar feeders affect bat-plant interactions in an Ecuadorian cloud forest? Dryad Digital Repository. <https://doi.org/10.5061/dryad.007s8>.
- MCCAFFREY, R. E., AND S. M. WETHINGTON. 2008. How the presence of feeders affects the use of local floral resources by hummingbirds: A case study from southern Arizona. *Condor* 110: 786–791.
- MOLINARI, J., AND H. MANTILLA-MELUK. 2016. *Anoura cultrata*. The IUCN Red List of Threatened Species 2016: e.T1566A22107379. Downloaded on 13 September 2016.
- MUCHHALA, N. 2006. The pollination biology of *Burmeistera* (Campanulaceae): Specialization and syndromes. *Am. J. Bot.* 93: 1081–1089.
- PERRET, M., A. CHAUTEEMS, R. SPICIGER, M. PEIXOTO, AND V. SAVOLAINEN. 2001. Nectar sugar composition in relation to pollination syndromes in Sinningieae (Gesneriaceae). *Ann. Bot.* 87: 267–273.
- ROUBIK, D. W., AND P. MORENO. 1991. Pollen and spores of Barro Colorado Island [Panama]. *Monographs in systematic botany from the Missouri Botanical Garden*, 36.
- SOLARI, S. 2016. *Anoura caudifer*. The IUCN Red List of Threatened Species 2016: e.T88108473A88185102. <https://doi.org/10.2305/iucn.uk.2016-1.rlts.t88108473a88185102.en>. Downloaded on 13 September 2016.
- SONNE, J., P. KYVSGAARD, P. K. MARUYAMA, J. VIZENTIN-BUGONI, J. OLLERTON, M. SAZIMA, AND B. DALSGAARD. 2016. Spatial effects of artificial feeders on hummingbird abundance, floral visitation and pollen deposition. *J. Ornithol.* 157: 573–581.
- TSCHAPKA, M. 2004. Energy density patterns of nectar resources permit coexistence within a guild of Neotropical flower-visiting bats. *J. Zool.* 263: 7–21.
- VON HELVERSEN, O., AND Y. WINTER. 2005. Glossophagine bats and their flowers: Costs and benefits for plants and pollinators. *Bat Ecol.* pp. 346.