Do nectar feeders in Andean nature reserves affect flower visitation by hummingbirds?

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Abstract

The interactions among plants and pollinators are crucial for plant reproduction because they structure gene flow among individual plants and among populations of plants. Throughout the Neotropics there has been a strong increase in recent years in the use of artificial nectar feeders in private nature reserves to encourage ecotourism through prolonged observations of hummingbirds. Currently, there is considerable uncertainty whether artificial feeders have a detrimental effect on plant reproduction through competition or a beneficial effect through facilitation. This uncertainty is disconcerting given that nature reserves harbour many rare and endangered plants whose successful reproduction is a conservation goal. To assess whether nectar feeders affected hummingbird visitation to flowering plants, we determined visitation rates in ten flowering species in five Andean nature reserves in Ecuador. We found that visitation rates tended to be higher within 5 m around the feeders than they were at 100 m, 500 m, or 1.5 km distance to the feeders, therefore indicating that nectar feeders tended to facilitate flower visitation at close distance. Because visitation rates at 100 m and 500 m distance from the feeders did not differ from those at 1.5 km, we suggest that feeders do not draw hummingbirds away from flower resources, but if they have an effect on flower visitation at all, they tend to facilitate flower visitation rather than reduce plant reproduction.

Zusammenfassung

Pflanze-Tier-Interaktionen spielen eine wichtige Rolle bei der Reproduktion von Pflanzen, da sie den Genfluss zwischen Individuen und Populationen räumlich strukturieren. In den letzten Jahren werden in privat geführten Naturreservaten der Amerikas verstärkt künstliche Nektarquellen (sog. nectar feeder) eingesetzt, um Ökotouristen durch die Beobachtung von Kolibris anzulocken. Momentan besteht jedoch Unklarheit darüber, ob die künstlichen Nektarquellen in Konkurrenz zu den Blüten stehen und somit die Fortpflanzung kolibribestäubter Arten einschränken oder ob sie aufgrund einer erhöhten Häufigkeit von Kolibris einen begünstigenden Effekt auf die Bestäubung von Pflanzen ausüben. Diese Unsicherheit ist beunruhigend, da Naturreservate oft eine Vielzahl seltener und bedrohter Pflanzenarten beherbergen, deren Fortpflanzung Ziel von Naturschutzbemühungen ist. Um beurteilen zu können, ob künstliche Nektarquellen die Kolibribesuche an Pflanzen beeinflussen, haben wir die Besuchsraten an zehn verschiedenen Pflanzenarten in fünf Naturreservaten der ekuadorianischen Anden bestimmt. Wir fanden heraus, dass die Besuchsraten in der direkten Umgebung der Fütterungsstellen gegenüber denen in 100 m, 500 m oder 1,5 km Entfernung tendenziell erhöht waren. Unsere Ergebnisse zeigen, dass künstliches Nektarangebot die Blütenbesuche in unmittelbarer Nähe

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tendenziell positiv beeinflusst. Da sich die Besuchsraten in 100 m und 1,5 km Entfernung nicht unterschieden, scheint künstliches Nektarangebot die Kolibris nicht von der Nutzung von Blütenressourcen abzuhalten. Dies deutet darauf hin, dass die künstlichen Nektarquellen in den fünf andinen Naturreservaten keinen benachteiligenden, sondern, wenn überhaupt eher einen begünstigenden Einfluss auf die Blütenbesuchsraten haben.

Keywords: Plant reproduction; Plant–animal interactions; Plant conservation; Ecotourism

Introduction

Plant–pollinator interactions are crucial for 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, Dajoz, Meriguet, & Loreau 2006; Gegear & Burns 2007). Hummingbirds represent the most important avian pollinators in the Americas. They pollinate about 10–15% of plant species in Neotropical biodiversity hotspots such as Ecuador (Feinsinger 1983; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent 2000). Because of their often beautifully coloured plumage, hummingbirds are commonly lured by artificial nectar feeders to encourage ecotourism. This can influence the abundance and distribution of hummingbirds and may thus affect pollination success of nearby flowering plants (Wethington & Russel 2003; Arizmendi, Constanza, Lourdes, Ivonne, & Edgar 2007; McCafferey & Wethington 2008).

Plants can show striking morphological adaptations to their main pollinators, resulting in specific pollination syndromes (Temeles & Kress 2003; Fenster, Armbruster, Wilson, Dudash, & Thomson 2004). The hummingbird pollination syndrome is generally described by long tubular, red flowers with a reduced labellum producing a high nectar volume (Wilson, Castellanos, Hogue, Thomson, & Armbruster 2004; Kay, Reeves, Olmsted, & Schemske 2005). However, hummingbirds can also be important pollinators for flowers with a different morphology. Although syndromes are often not exclusive, morphological adaptations to one type of pollinator can lower the efficiency of other types of pollinators (Fenster et al. 2004). Anthers and stigmas for example, may be positioned so that they directly touch the forehead of a hummingbird probing the flower for nectar, which can result in a lower likelihood of making contact with bees crawling into the corolla (Castellanos, Wilson, & Thomson 2003). Furthermore, nectar amount and sugar concentration are considered important adaptations in the evolution of plants towards the taste and energy requirements of their pollinators (Dupont, Hansen, Rasmussen, & Olesen 2004). Flowers adapted to hummingbirds usually secrete high volumes of nectar with sugar concentrations ranging from 16 to 28% (Stiles & Freeman 1993; McDade & Weeks 2006). Sugar composition is mostly dominated by sucrose which is preferred by hummingbirds over glucose and fructose (Martínez del Río 1990).

For plants primarily relying on one guild of pollinator, the pollination process can be disrupted if those pollinators are offered alternative food supply and are thus drawn away from flowers. Because the abundance of floral resources is known to influence the number of hummingbirds visiting nectar feeders (Inouye, Calder, & Waser 1991), it is likely that feeders also affect the patterns of flower visitation by hummingbirds (McCaffrey & Wethington 2008). Owing to the increased food supply, feeders can raise local hummingbird abundance (Wethington & Russell 2003). However, it remains unclear whether this increased occurrence of hummingbirds translates into higher visitation rates to plants. Because of the enormous quantities of nectar that feeders provide, they could outcompete local flowers and thereby lower their seed production as shown by Arizmendi et al. (2007) in a suburban park in Mexico. It is unclear whether the results by Arizmendi et al. also hold for more complex ecosystems where the abundance of flowers and hummingbirds vary temporally and spatially.

The current uncertainty on the effect of feeders on plant–pollinator interactions is unsettling. In particular, the growing ecotourism market in the Neotropics led to an increasing use of nectar feeders in nature reserves that often protect crucial remains of endangered ecosystems. For example, most privately owned reserves in the Mindo region of North-western Ecuador now use feeders (TB and HMS pers. obs.) because these allow tourists prolonged observation of hummingbirds that are often considered to be particularly attractive. The importance of hummingbird pollination for plant communities in the Ecuadorian Andes has been documented for cloud forest habitats (Dziedzioch, Stevens, & Gottsberger 2003). The high degree of endemism in the Andes of Ecuador (Borchsenius 1997) entails that nature reserves usually harbour rare and endemic plants whose reproduction is an important conservation goal (Morawetz & Raedig 2007) that might be thwarted by the use of artificial nectar feeders.

Our study aims to examine the general effect of feeders on plant–hummingbird interactions in natural and highly diverse environments. More specifically, we examined two mutually exclusive hypotheses. Our first hypothesis is that feeders reduce hummingbird visitation to flowers (see Arizmendi et al. 2007), whereas the second hypothesis is that feeders are neutral to, or increase the rate of flower visits because they augment the overall population density of hummingbirds. Although a visit to a flower does not necessarily mean that pollination takes place, the frequency of visits of potential pollinators enhances the likelihood of pollen transfer and may thus be used as a proxy (Engel & Irwin 2003). Based
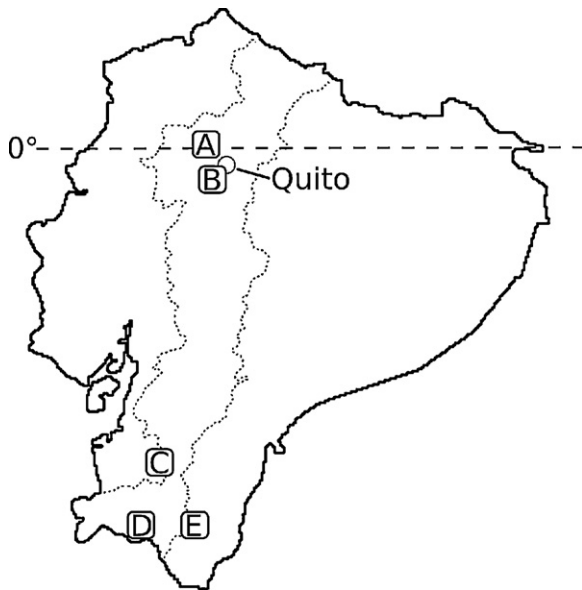
Fig. 1. Schematic map of Ecuador, dotted lines represent the boundaries of the Andean range; letters indicate geographical position of the study sites: A, Mindo – Loma; B, Yanacocha; C, Buenaventura; D, Utuana; and E, Tapichalaca.

on the first hypothesis we predicted that hummingbirds pay fewer visits to flowering plants close to artificial feeders. Alternatively, the second hypothesis posits that the frequency of flower visits increases or remains constant with decreasing distance from the feeders. To test the generality of these hypotheses, we assessed the effect of nectar feeders on hummingbird visits to ten hummingbird-pollinated plant species in five cloud forest nature reserves in the Andes of Ecuador.

Methods

Study sites

Study sites were forest reserves protecting cloud forest habitats at different altitudes ranging from 450 m to 4000 m above sea level (a.s.l.) on both sides of the Andes (Fig. 1). Two reserves are located in northern Ecuador and three in southern Ecuador; all except one reserve belong to Fundación Jocotoco.

Buenaventura-Reserve protects low altitudinal cloud forest located on the western slopes of the southern Andes of Ecuador (Province El Oro). This reserve ranges from an altitude of 450–1100 m a.s.l. and feeders are located at an elevation of 550 m. Tapichalaca Reserve is on the eastern flanks of the southern Andes in the Province of Zamora-Chinchipe and it protects 2000 hectares (ha) of cloud forest including a high proportion of bamboo ranging from 2000 m a.s.l. up to páramo vegetation at 3400 m a.s.l.; here feeders are located at 2500 m a.s.l. With an annual precipitation of 5000–8000 mm per year, Tapichalaca is the most humid of

the reserves studied. Utuana is a small reserve of dry evergreen forest at an altitude of 2500 m a.s.l. located near the border of Peru. It has the lowest precipitation compared to the other reserves. Mindo Loma-Reserve is located on the western flanks of the Andes near Quito (Province Pichincha) and consists of primary and secondary mid-elevation cloud forest at elevations of 1750–1950 m a.s.l.; here feeders are located at 1800 m a.s.l. Yanacocha-Reserve lies on the slopes of the Volcan Pichincha near the Ecuadorian capital Quito and protects 964 ha of high-altitude cloud forest from 3300 m to 4000 m a.s.l., including a high proportion of *Polylepis* trees; here feeders are located at 3500 m a.s.l.

Given that some of the reserves were located on the east slope and some on the west slope and that they all differed in elevation, we expected the hummingbird and plant communities to also vary among the reserves. Rather than comparing species-specific responses in our experimental design, we were interested to evaluate whether the presence of feeders consistently changed the pollination behaviour of the hummingbird community in spite of the variation in species composition among the reserves.

Experimental design

In each of the reserves several feeders were located near a lodge within the reserve or near its entrance. There were no other feeders within or in the vicinity of the reserves, and they usually have been maintained for several years before the study. Although the number of feeders was not the same in all reserves, they were always positioned at one spot forming a concentrated and reliable source of nectar. All the feeders in the reserves contained a 1:10 sugar solution (10% mass–volume–percentage) provided daily by the reserves' employees. This concentration of sugar was used by the owners of the reserves to attract hummingbirds. It was therefore constant over a very long time period before the experiments. Feeders were constantly kept full during the study period.

From October 2008 to February 2009 we recorded visitation rates of all hummingbirds to flowers in four distance classes relative to the feeders: (1) close to the feeder (within 5 m radius from the feeder), (2) approximately 100 m (distances ranged from 80 m to 120 m from the feeder), (3) approximately 500 m (with distances from 450 to 500 m), and (4) one control, at least 1.5 km away, which we assumed to be unaffected by the feeders. Generally, we expected the influence of the feeders on the abundance of hummingbirds to decrease with increasing distance to them. There is considerable variation in hummingbird behaviour, with some species defending small territories, some species following valuable resources over larger areas (trap-lining), and non-territorial species. In territorial species, territory size can vary ten-fold according to resource value (up to 3200 m^2), but often lies within 100–250 m^2 (Kodric-Brown & Brown 1978; Hixon, Carpenter, & Paton 1983; Jacobi & Antonini 2008). Since we observed that all plant species were visited by

Table 1. Hummingbird visitation rates per hour in the four distance classes for the ten observed flowering plant species. The species are ordered by the reserve they were observed in.

Reserve/genus	Feeder	100 m	500 m	Control
Yanacocha				
Fuchsia	0.22	0.00	0.00	0.22
Centropogon	0.44	0.00	0.00	0.22
Tapichalaca				
Guzmania	3.67	0.00	0.17	0.83
Bomarea	0.33	0.00	0.33	0.00
Buenaventura				
Tillandsia	7.67	0.67	0.67	0.67
Vriesa	3.67	0.17	0.00	0.33
Mindo-Loma				
Kohleria	0.00	1.40	0.00	0.29
Centropogon 2	0.20	0.00	0.50	0.25
Axinea	3.00	5.71	1.00	0.28
Utuana				
Oreocallis	2.33	2.00	4.00	2.00

multiple hummingbird species (Appendix A), it is unlikely that the observed floral visitation patterns were predominantly influenced by single individuals and species. Owing to the diversity of foraging strategies among hummingbirds, we predicted the inverse relationship between distance to feeders and influence of those feeders on hummingbird behaviour to be gradual rather than stepwise. We therefore chose three distance classes that were well separated spatially and that had a decreasing likelihood of being dependent on the presence of feeders.

Because we were interested in a general effect of the presence of feeders, we observed ten plant species (on average two in each of the five reserves, with the exception of only one species in Utuana and three species in Mindo-Loma) differing in flower morphology (Table 1). All species were known to be visited regularly by hummingbirds. We determined in preliminary observations that visiting hummingbirds approached the flowers in a way that makes pollination likely. Owing to the steep terrain of Andean forests, the observed plant individuals in the respective distance classes were not randomly distributed around the feeders. First, we made all observations at the same altitude of the feeders (± 100 m) thereby restricting the direction relative to the feeders. Further, since the terrain is often inaccessible, we searched along the few trails of each reserve for plant individuals in each distance category. Within each distance category we selected the first suitable individual that we encountered. For each species, suitable individuals were defined so that the numbers of flowers per plant could be kept constant for all observed individuals (number depending on species; for herbaceous plants and Fuchsia: 1–2 open flowers; for trees one inflorescence with 3–5 open flowers was observed, while the rest of the open flowers was adjusted by removing the surplus flowers).

We likewise controlled the alternative flower supply provided by co-flowering plants in the vicinity of the focal individual to reduce biases caused by neighbourhood effects. Depending on site-specific overall flower supply, all co-flowering individuals within a radius of 10 m were kept constant by choosing adequate observation spots and if necessary by removing excess flowers. We chose a radius of 10 m here because there was a high likelihood of detecting hummingbirds in this area. If no individual of the focal plant species was found we transferred an adequate (in terms of number and condition of flowers) flowering individual from a nearby area that was not previously used in the experiment. Overall, we transferred 35% of all observed individuals. Transferred plants were placed in water buckets to keep them fresh and placed at the observation point one day before data collection. Transferred plants were not visited less often than plants growing at our experimental sites ($p > 0.65$). Observations were made with binoculars and with the help of a tripod-mounted Sony camcorder located at a distance of 5–10 m from the focal plant. Individuals of the plant species were photographed and identified to the level of genera in the Herbario Nacional de Loja.

Visitation rate was calculated as visits per hour. At each distance class we observed one individual of each of the plant species studied in each reserve. Observation time varied from at least 3 h up to a maximum of 6 h, cumulating to a total observation time that ranges between 15 and 24 h per species at each reserve. We observed each individual at least once during the morning after sunrise (within the period from 07:00 h to 10:00 h) and once in the evening before sunset (from 15:00 h to 18:00 h) when hummingbird activity was highest. For the two plant species in Buenaventura (*Tillandsia* spec., *Vriesa* spec.) visits were recorded only once, either in the morning or in the evening.

Statistical methods

Because our study design included different study sites and different plant species and each plant species was only observed at a single site, we cannot disentangle possible site-specific and species-specific effects on floral visitation. To address this situation we used several analyses: we converted visitation rates (visits/hour) into proportions in two different ways. First, we standardized the raw visitation rate of each distance class of a plant species on the sum of the visitation rates of all distance classes for this species. This allowed us to account for variation in total number of visits between plant species. Second, we standardized the visitation rate of all observations within a reserve on the sum of observed visits in that reserve to account for differences in visitation rates among reserves.

To assess whether floral visitation changed with increasing distance to the feeder we constructed three statistical models. We calculated a Kruskal–Wallis test on the reserve means ($n = 5$) for each distance class. This test was performed on

Table 2. The fixed effects table of the nested-ANOVA model. The parameter estimates are the best linear unbiased predictors. The intercept of the model represents values of the control distance and entries for the other distance classes refer to differences from the control.

	Estimate	Std. error	df	t-Value	p-Value
Intercept	0.3944558	0.1282515	20	3.0756421	0.0060
Feeder	0.3648465	0.1813751	12	2.0115583	0.0673
100 m	−0.1080563	0.1813751	12	−0.5957614	0.5624
500 m	−0.0779292	0.1813751	12	−0.4296578	0.6751

standardized data of reserves and plant species to account for possible site-specific and species-specific effects, respectively. Additionally, we ran a nested two-way ANOVA on the proportions of visits in each distance class so that all visits of a given plant species sum up to 1 (arcsine-transformed prior to analysis). Nesting the distance levels as fixed effects into reserves allowed us to raise the power of the test and to calculate estimates that were unbiased by autocorrelation within our data. All calculations were performed with R 2.13.0 (R Development Core Team 2011). The nested-ANOVA model was calculated using the lme()-function from the R-package nlme (Pinheiro et al. 2011).

Results

We found no significant effect of distance to the feeder on the visitation rate of hummingbirds (Kruskal–Wallis test on standardized plant species totals: $\chi^2 = 5.813$, $df = 3$, $p = 0.1211$). Likewise, the visitation rate differed only marginally if visitation was standardized on reserves (Kruskal–Wallis $\chi^2 = 6.857$, $df = 3$, $p = 0.0766$) or when analysed in a nested design (nested-ANOVA, fixed effects: $df = 12$, F-value = 2.8952, $p = 0.0791$, see Table 2). Interestingly, distance effects explained more than 30% of variance in our data in all analyses (visitation standardized on plant species totals $\eta^2 = 0.301$, standardized on reserve totals $\eta^2 = 0.361$, nested-ANOVA $\eta^2 = 0.323$) thereby demonstrating that the results are consistent among the different statistical approaches.

The marginal effects visible in two analyses (Kruskal–Wallis test standardized on reserves and nested ANOVA) are caused by visitation close to the feeder (Table 2), which is most different from the visitation rates at any other distance class. It is important to note in this context, however, that the Kruskal–Wallis test, particularly, can be biased by species-specific responses of a few plant species (namely, the Bromeliaceae, Table 1). This bias is excluded in the Kruskal–Wallis tests standardised on plant species, which showed no marginal effects. We finally note that the variance explained by reserves was negligible ($\eta^2 < 0.0001$) in the nested-ANOVA if corrected for plant species differences in visitation rates. This shows that differences in visitation among plant species accounted for almost all variation attributable to either differences in plant species or reserves.

Discussion

We found no significant differences in hummingbird visitation rates of flowers at different distances to the feeders. We purposely included very different plant and hummingbird species in our analyses. Our conclusion that there are no general effects of nectar feeders on hummingbird visitation may not hold for all plant species. If there are any effects of nectar feeders in Andean reserves, we expect them to facilitate local plant visitation rates around the feeders rather than to outcompete the surrounding plants. Such an effect may be possible because feeders can increase the local abundance of hummingbirds.

Our results that there are no overall effects of nectar feeders on hummingbird visitation is in contrast to the results by Arizmendi et al. (2007), who found that the presence of feeders in an urban park in Mexico can lower visitation rates of three hummingbird species to two plant species of the genus *Salvia* and also affect seed set in one *Salvia* species. The contrasting results might be explicable by the very high hummingbird abundance at the feeders we observed (mostly >20 individuals simultaneously present). The high abundance coupled with the territorial behaviour of some species prevented that all of the hummingbirds present around the feeders could simultaneously drink at them. Aggressive behaviour of hummingbirds such as fights and chases is very common at feeders (*e.g.* Pimm, Rosenzweig, & Mitchell 1985; pers obs.). Because competition can lead to an increasing use of suboptimal resources by subordinate hummingbird species (Pimm et al. 1985), it likely represents the proximate mechanism why feeders do not outcompete surrounding flowering plants in the Ecuadorian nature reserves we visited.

A further likely reason for the neutral effect of the nectar feeders is that their sugar concentration was more diluted than that of most hummingbird pollinated flowers (*e.g.* Stiles & Freeman 1993). This might also explain why flowers were visited in the presence of feeders. This is consistent with the results of previous studies reporting a negative correlation between the abundance of flowers and visitation to feeders (Inouye et al. 1991; McCaffrey & Wethington 2008). Because the sugar concentration of the feeders at our study sites was half that of the commonly employed 20%-solution, this difference might contribute to explain the contrasting results of our study and that by Arizmendi et al. (2007). In this case, manipulating sugar concentration might be an interesting management approach to secure pollination services in nature reserves.

Our data do not support a scenario that feeders had such a magnet effect in attracting hummingbirds that overall floral visitation rate dropped in 100 m or 500 m distance to the feeders relative to the visitation pattern at 1.5 km distance.

This conclusion rests on the assumption that the visitation rate at 1.5 km distance of the feeders (our control) was unaffected by the presence of the feeders. Given that the known size of hummingbird territories are usually within the ranges of a few hundred m^2 and rarely exceeding $3200\,m^2$ (*e.g.* Kodric-Brown & Brown 1978), it seems that this is a reasonable assumption for the entire hummingbird community, even though home ranges and foraging routes of trap-lining hummingbird species might be considerably larger than defended territories.

It is important to note that the patterns of floral visitation varied according to plant species (Table 1). The species-specific responses to feeder presence entails that our conclusion on the neutral effect of feeders may not hold for all species visited by hummingbirds within plant communities. Table 1 shows that some species were less often visited at 100 m distance to the feeders than at 500 m or 1.5 km distance, while two plant species (*Kohleria* spec. and *Axinea* spec.) show a pronounced peak in visitation rate at 100 m. These results remain unexplained by our data and might be the result of more complex inter-specific interactions between hummingbirds and plants in the presence of feeders.

Overall, we conclude that the common practice of providing artificial feeders to lure hummingbirds did not result in an overall lower floral visitation rate of hummingbirds in five Andean cloud forest reserves. But it should be cautiously noted that the high variance resulting from a taxonomically and phenotypically diverse data set may mask effects on more specific interactions between smaller groups of species.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2012.02.005.

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