Reproductive biology and effect of nectar robbing on fruit production in *Macleania bullata* (Ericaceae)

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Abstract

Hummingbird-pollinated flowers are frequently subjected to nectar robbing. In this paper, I examine the impact of nectar robbing on plant reproductive success on a hummingbird-pollinated species. After studying the basic aspects of the floral morphology and reproduction of *Macleania bullata* (Ericaceae) in a tropical montane wet forest in southwest Colombia, I examined the percent of flowers robbed and the effect of nectar robbery on fruit set. The flowers of this species are typical for plants pollinated by long-bill hummingbirds. They are protandrous and open for four days. Fruit production requires a pollinator visit; fruit set following pollinator exclusion was zero. Fruit set following xenogamous pollen transfer (36.8%) differed significantly from that of population controls (11.9%) and of autogamous pollen transfer (6.3%). Nectar volume, sugar concentration and sugar production were measured at daily intervals from bud opening until the fading of flowers. Daily nectar production (both volume and amount of sugar) varied considerably with flower age. Sugar production peaked on the second day, coinciding with the male phase. The frequency of nectar robbing in the studied population was very high (75% of examined flowers) and was positively correlated with reduced fruit set. I discuss the probability of a relation between reduced fruit set on robbed flowers and an energetic investment. Robbing by non-pollinating visitors can suppose the plant to re-synthesize more nectar. The high incidence of nectar robbing impugns the advantage of specialization.

Introduction

Pollination syndromes (*sensu* Faegri & van der Pijl 1979) describe harmonic relationships between subsets of plants and their pollinators, based on conformity of morphological and physiological traits. Thus, it has been widely held that tubular flowers with long and narrow corollas of orange/red color which produce high quantities of nectar should be pollinated by long-billed hummingbirds (see however Herrera 1996; Waser et al. 1996). However, in recent years, detailed studies on interactions between flowers and their visitors have revealed the importance of floral visitors that are not adapted to floral morphology, but obtain nectar by piercing floral tissues without contacting the anthers and stigma. These visitors are called nectar robbers (see Inouye 1983 for terminology of different types). A growing number of studies show that plants with 'bird-pollinated' morphologies suffer the visits of nectar robbers (McDade & Kinsman 1980; Willmer & Corbet 1981; Carpenter et al. 1993; Powers & Conley 1994; Bittrich & Amaral 1996; Arizmendi et al. 1996; Traveset et al. 1998; Irwin & Brody 1998). In spite of the common occurrence of nectar robbing by birds, studies evaluating their effects on plant reproductive performances are scarce (see Waser 1979; McDade & Kinsman 1980; Arizmendi et al. 1996; Traveset et al. 1998; Irwin & Brody 1998). Nectar robbers may generate a cost to the plant in terms of reduced reproductive success. Some studies show either damages to floral tissues inflicted by robbers (McDade & Kinsman 1980; Galen 1983), or reduced attractiveness of robbed flowers to legitimate pollinators (Heinrich 1976; Roubik 1982; see, however, Free & Butler 1959; Hawkins 1961; Soberón & Martínez del Río 1985; Cushman & Beattie 1991; Morris 1996).

Although Ericaceae are prominent features of tropical montane forest throughout the world, they are,

paradoxically, poorly known ecologically or biologically (Luteyn 1989). Virtually no investigations have been made of tropical Ericaceae concerning breeding systems and pollination ecology (however see Melampy 1987, Navarro 1999). Nevertheless, this family includes many genera which conform to hummingbird pollination syndromes.

Studying the pollination ecology of *Macleania bullata* (Ericaceae) and the effect of nectar removal on new nectar synthesis, I found that *M. bullata* is visited by nectar-robbing hummingbirds. In addition, experimental removal of nectar showed a re-synthesis of nectar. Thus, nectar removal resulted in an increase in total volume of nectar produced over the flower lifespan, but did not affect mean sugar concentration (Navarro 1999). This could suppose an energetic extra-investment to the plant. The principal aim of this paper was to provide information concerning the mating system of this plant species and to examine the effect of nectar robbing on fruit production. In this way, I hope to make a contribution to the knowledge of the effect on nectar robbing of hummingbird pollinated flowers. To this end, I firstly examine the floral morphology and provide information concerning the mating system of this prominent plant species in montane tropical forest. I studied affect of level of selfing versus outcrossing on fruit set and the effect of nectar robbing on fruit set levels. Finally, based on available data, I discuss possible causes of these results.

Study area and plant

The study was carried out in the *Reserva Natural La Planada*, near the village of Ricaurte (Departamento de Nariño, Colombia) (1°10′ N; 77°58′ W). The reserve is located on the western flank of the Andes, and comprises 3200 ha of montane wet forest (bmh-PM *sensu* Holdridge 1996) at altitudes between 1200 and 2100 m. Mean annual precipitation is 4375 mm (Carlos Valderrama, pers. comm.), and annual mean temperature ranges between 12 °C and 23 °C.

Macleania bullata Yeo (Ericaceae) is a climbing shrub or epiphyte which, in the study area, typically forms part of the fringe community around mature forest. It has several flowering peaks during the year. The flowers are hermaphroditic with a fleshy, long, orange-red, zygomorphic corolla tube. The stigma is slightly exerted and the anthers are below the style. The main 'legitimate' flower visitors are traplining hummingbirds *Coeligena torquata* and *Doryfera ludoviciae*,

although a high percent of visitors are nectar robbing species of hummingbirds and bees. In fact, the main floral visitors are two nectar-robbing hummingbirds, *Ocreatus underwoodii* and *Chlorostilbon mellisugus*, and bees of the genus *Trigona*. Nectar robbers can be divided into primary nectar robbers (represented by the birds *C. mellisugus*, *Aglaiocercus coelestis* and *Diglossa cyanea*, data from Navarro 1999), which make a hole in the corolla tube to extract the nectar (29% of visits) and secondary nectar robbers (the hummingbird *O. underwoodii*, the bee *Trigona* sp., and butterflies of *Pronophila orcus* species, data from Navarro 1999), which take advantage of a previously made hole (42% of visits). Robbers' bills is not longer than 15 mm. During the process of nectar robbing, none of the robbers appear to make contact with the anthers and/or the stigma of the flower (Navarro 1999). In addition, nectar robbery does not cause substantial damage to the plant's sexual organs. Although legitimate pollinator activity occurs early in the day, nectar robbers maintain their activity throughout the day. Robbed flowers are re-visited after robbery because they continue nectar synthesis (Navarro 1999). The fruit is a translucent white berry, which is probably eaten by frugivorous birds. Voucher specimens of *M. bullata* from the study site are deposited at the herbarium of the Universidad de Pasto in the Departamento de Nariño, Colombia.

Methods

Floral morphology

In order to infer which are the morphological characteristics that pollinators need to visit this plant species legitimately, I measured corolla length, and corolla width at the opening of the tube on 20 flowers (one per plant). Moreover, to examine the presence of herkogamy, style and stamen length was also measured.

Floral duration

To investigate floral duration I marked a total of 20 flowers (one per plant), before they opened and monitored them daily for eleven days.

Pollen germinability

To verify whether or not this species presents true dichogamy, pollen germinability and stigma receptivity

were examined. I bagged 50 flowers with mosquito netting prior to opening. I then collected pollen from 10 flowers in each of these categories: unopened buds (hereinafter day 0), 1 day post opening (day 1), 2 day post opening (day 2), 3 day post opening (day 3), and 4 day post opening (day 4). The pollen was immediately placed in Petri dishes on a sterile solid medium (as per Bar-Shalom & Mattson 1977) containing 10% sucrose (this being the concentration which gave the highest germination rate in preliminary tests with 10, 20, 30 and 40% sucrose). The pollen was incubated for 4 h. and germination counts (1000 grains per flower) were carried out under a stereo microscope. All grains with pollen tube length longer than the grain diameter were counted as 'germinated'.

Stigma receptivity

To investigate the time of stigma maximum receptivity, I used peroxidase test paper (Peroxtesmo Ko, Mackerey-Nagel, Cat. No. 90606) on flowers from 0 to 4 day old (one flower per plant). If the stigma is receptive as indicated by the presence of peroxidase, the peroxidase test paper changes color (Kearns & Inouye 1993).

Nectar production

To investigate nectar production, I bagged 57 randomly chosen flowers on 18 plants and, after 24 h, determined nectar volume in each flower with a capillary micropipette. I also determined sugar concentration on site with a portable refractometer (Fisher, mod. 0–32%). On the basis of these data I estimated (as per Cruden & Hermann 1983) the amount of sugar produced by each flower in 24 h. Nectar was extracted without removing the flower from the plant and always at about 09:00 a.m. To avoid the obstruction of the capillary micropipette with flower's pollen, I made a hole with a jack-knife in the base of each corolla tube from which I extracted the nectar.

To investigate possible variation in nectar secretion patterns with flower age, nectar was measured in flowers aged 0, 1, 2, 3 and 4 days, defining day 0 as the day on which the flower opened. For this experiment 10 flowers in each age class ($n = 50$ flowers) were randomly chosen from 10 plants. These were labeled when open and bagged with mosquito netting 24 h before they were due to be examined. The nectar was extracted with a capillary micropipette, and sugar concentration was determined, on site, with a portable refractometer.

Nectar robbery

A total of 1000 flowers on 172 plants were monitored for fruit set. I noted whether or not each flower was robbed and, after approximately one month, whether or not it initiated a fruit. Field determination of whether a flower has been robbed or not is straightforward, since the robber leaves a clearly visible incision in the corolla. The robbed flowers present a unique hole independently when they have been robbed more than once. To examine if robbed flowers set fruit or not, I marked stems from each flower with a little mark of indelible ink. I used blue and red ink for robbed and not robbed flowers, respectively.

Determination of mating system

The importance of outcrossing was examined using flowers from 16 labeled branches on 4 individuals (4 branches on each individual). Control of the population was recorded from another branch of those treated individuals, and from a branch in an additional individual. Flowers were treated as follows.

- Insect exclusion: bagged with mosquito net ($n = 68$ flowers from four branches, one branch per individual with a mean of 17 ± 5 flowers by branch).
- Autogamy: bagged with mosquito net and pollinated with pollen from the same flower ($n = 26$ flowers from three branches from three individuals with a mean of 13 ± 3 flowers by branch). Note that in this experiment one branch was lost.
- Xenogamy: bagged flowers carefully emasculated and pollinated with pollen from another plant ($n = 38$ flowers from four branches from four individuals with a mean of 10 ± 6 flowers by branch).
- Supplementary pollination: flowers pollinated with pollen from another plant and not bagged ($n = 62$ flowers from four branches from four individuals with a mean of 16 ± 3 flowers by branch).
- Control: no treatment ($n = 59$ flowers from five branches from five individuals with a mean of 12 ± 3 flowers by branch).

In all cases, branches were randomly selected and hand-pollination was carried out daily after anthesis. It was not possible to have a larger sample because it was difficult to isolate more individuals on the study

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area. Fruit set was recorded after approximately two months.

Data analysis

Nectar data were compared using a randomized block design analysis of variance in which individual plants were treated as block and each flower age as experimental units, each of which corresponded to one of the five levels of the flower age. Sugar concentration data were arcsine transformed before statistical analysis to increase normality. The possible effects of nectar robbing on the probability of a flower setting fruit were examined using the chi-squared test on data arranged into a contingency table, with $p < 0.05$ being taken as significant. The number of surveyed plants ($N = 172$) was considered big enough to apply χ^2 test. The effect of pollen treatments on fruit set was assessed by fitting a generalized linear mixed model to the data using SAS macro GLIMMIX (e.g., Herrera 2000). Pollen treatment was treated as a fixed effect, and individual plants were incorporated into the model as a random effect. Estimates of fruit set (= fruits/flower) were modeled using logits and the binomial probability distribution. Specific a priori hypotheses were tested using appropriate CONTRAST statements. In the text, mean values are cited with their standard deviation.

Results

Floral morphology

Mean morphological measurements are shown in Table 1. The mean length of the corolla tube was 42.4 mm and the style slightly exceeded the rim of the corolla. The anthers remain 30 mm below the stigma. Thus, pollinators encounter the stigma first and then anthers before reaching nectar that is secreted at the bottom of the corolla. Access to the interior of the flower for a 'legitimate' visitor is only possible from the apex. The narrow diameter of the corolla tube only allows an access to the interior to those visitors with bill or body diameter shorter than 5 mm. Moreover the fleshy consistency of the corolla prevents tearing by visitors with bigger bodies.

Floral duration

Mean floral lifespan was 3.7 ± 0.6 days ($n = 20$ flowers). Anther dehiscence occurred when the flowers opened but maximum pollen germination did not

Table 1. Floral characteristics of flowers of *Macleania bullata*.

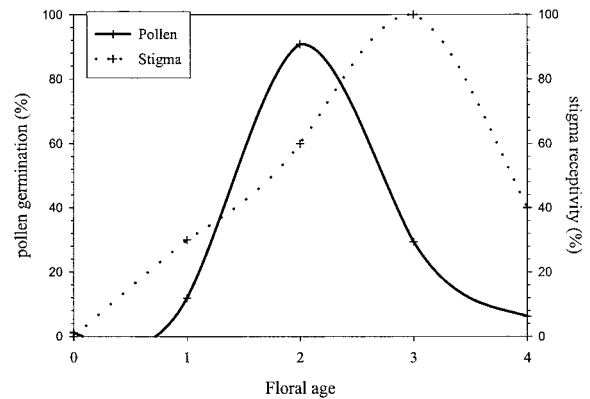|	Mean ± std	Range	N
Corolla length (mm)	42.4 ± 2.0	37.9–46.2	20
Corolla width (mm)	4.7 ± 0.7	3.9–5.9	20
Style length (mm)	43.8 ± 3.8	31.1–48.9	20
Stamen length (mm)	15.1 ± 1.5	12.6–18.0	20

Figure 1. Time course of pollen germination and stigma receptivity with flower age.

occur until the second day (Figure 1). Most stigmas were not receptive until the third day (Figure 1). Thus, the flowers seem to be protandrous.

Nectar production

Nectar was located exclusively at the bottom of the corolla tube. The mean volume of nectar produced by a flower in 24 hours was 33.7 ± 9.1 μl, and its mean sugar concentration was $18.6 \pm 1.7\%$ w/w.

Nectar secretion was continuous throughout the life of flowers. Buds contained a small amount of nectar (ca. 1 μl) (Figure 2). Nectar production varied significantly with flower age ($F_{4,36} = 63.4$, $p < 0.0001$), but it was not affected by the plant factor ($F_{9,36} = 1.9$, $p = 0.0848$). As can be seen in Figure 2, nectar production peaked during the male phase. Sugar concentration in nectar did not vary significantly with flower age ($F_{4,27} = 2.0$, $p = 0.1277$). The plant factor also had no effect on sugar concentration ($F_{9,27} = 0.4$, $p = 0.9399$) (Figure 2).

Nectar robbery

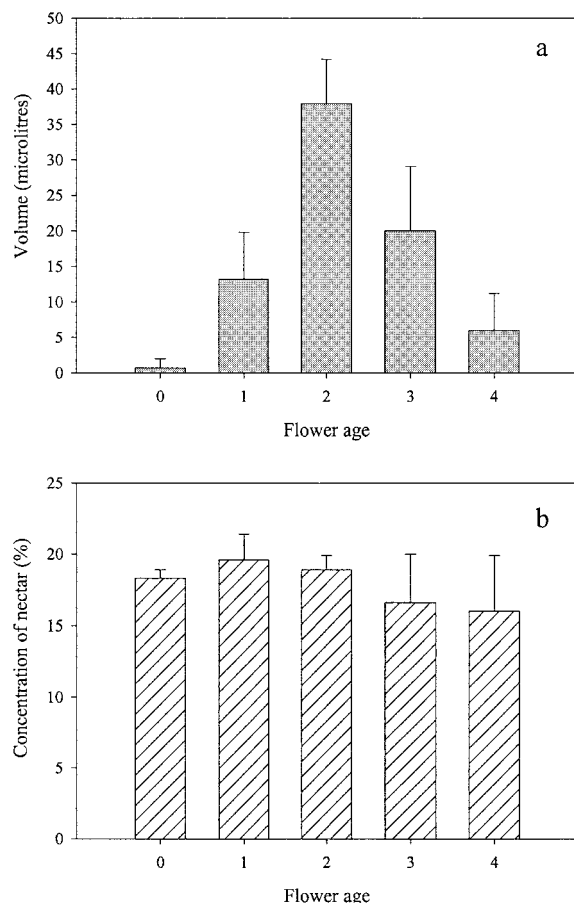Nectar robbers pierced 74.9% of the marked flowers. Flowers that were not robbed set fruit more frequently

Figure 2. (a) Nectar production rates throughout the lifespan of the flower and (b) Sugar concentration in nectar throughout the lifespan of the flower.

Figure 3. Fruit set level obtained in flowers of *Macleania bullata* treated as follows: B = bagged with mosquito netting, C = control (no treatment), A = autogamous pollen transfer, X = xenogamous pollen transfer, SP = supplementary pollination. Mean are shown with standard deviations; columns with the same letter do not differ significantly.

crease fruit set over control plants ($F_{1,11} = 3.0$, $p = 0.111$).

Discussion

The results indicate that the morphology of flowers of *M. bullata* only permits legitimate access to the nectar to a limited group of long-billed, long-tongued species or to visitors with a body diameter shorter than 5 mm. This characteristic combined with stoutness, red color, lack of odor, and the production of large amounts of low concentrated nectar conform the 'hummingbird-pollination syndrome' (*sensu* Faegri & van der Pijl 1979). Flowers from which visitors were excluded by bagging did not produce fruit. This suggests that spontaneous autogamy on *Macleania bullata* is prevented by spatial separation between stamens and stigma and/or by protandry. Despite being dependent on pollinators, fruit set was not limited by pollinator or pollen availability, as indicated by the comparison between supplementary pollination experiments and the population control. Two traplining hummingbirds, *Doryfera ludoviciae* and *Coeligena torquata* (Navarro 1999) pollinate flowers of this species. These hummingbirds visit only a few flowers per plant in their long foraging flights causing an important degree of xenogamy (Feinsinger & Colwell 1978; Handel 1983). However, fruit set following the experimental xenogamy treatment was significantly higher than in control and in pollen supplemented flowers. Note that control and pollen supplemented flowers were un-

than robbed ones: 28.7% ($n = 206$ flowers) versus 8.2% ($n = 614$ flowers) ($\chi^2 = 35.7$, $p < 0.0001$). During this experiment 7.7% of the flowers were lost by herbivory and 10.3% rotted. All rotted flowers contained beetle larvae (Curculionidae) in the interior of corolla tube. The larvae eat the fleshy tissues of the corolla causing deterioration of the flower.

Determination of mating system

Mean fruit set in control plants (not receiving either pollen addition or pollinator exclusion treatments) was $11.9 \pm 3.7\%$. The results (Figure 3) show that pollinator visits were required for reproduction. No fruit was set following pollinator exclusion. Xenogamous pollen transfer resulted in significantly higher fruit set than autogamy ($F_{1,11} = 57.2$, $p < 0.001$) or pollen supplemented treatment ($F_{1,11} = 35.2$, $p < 0.001$). Supplementary pollination did not significantly in-
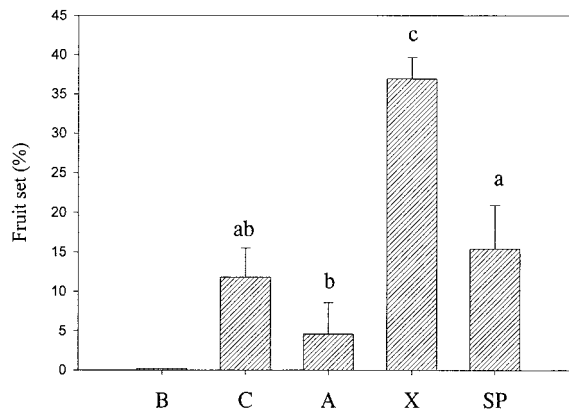
bagged and experienced frequent robbery suggesting that nectar robbing may be related to fruit set.

Similar nectar robbery has been recorded for other bird-pollinated flowers (McDade & Kinsman 1980; Willmer & Corbet 1981; Graves 1982; Carpenter et al. 1993; Powers & Conley 1994; Arizmendi et al. 1996; Bittrich & Amaral 1996), and a number of studies have revealed that nectar robbing has negative consequences for plant fitness. Robbers inflict damage to floral tissues and/or reduce the attractiveness of flowers to legitimate pollinators (Heinrich 1976; McDade & Kinsman 1980; Roubik 1982; Galen 1983; Irwin and Brody 1998). Nectar robbers on *M. bullata* extract nectar without contacting the sexual organs of the plant, consequently, reproductive tissue damage does not occur (Navarro 1999). However, robbing reduces temporarily the amount of nectar available to the legitimate pollinators. If the amount of nectar per flower is reduced, the behavior patterns of the legitimate pollinators could be altered (Wyatt 1980). A decrease in the amount of nectar during the flower's female phase could reduce the number of legitimate pollinator visits to these flowers. This may have dramatic consequences on fruit production. However, several reasons suggest that this is not the case: (1) experiments of pollen supplementation showed that under natural conditions robbed plants are not pollen limited; (2) legitimate pollinators visit flowers early in the morning when robber's activity is still low; and (3) experimental removal of nectar in this species stimulates an increase of nectar production without affecting mean sugar concentration (Navarro 1999). Therefore, robbed flowers may not differ in nectar standing crop compared to unrobbed flowers.

Nectar production can represent a considerable investment for plants that attract pollinators for reproduction (Southwick 1984; Pyke 1991 but see Harder & Barrett 1992). As a consequence of nectar robbery, plants secrete more nectar than would otherwise be required in order to maintain attractiveness to legitimate pollinators who transfer pollen effectively. Therefore, nectar replenishment can impose a high cost on the plant. By manipulating nectar production in *Blandfordia nobilis* flowers, Pyke (1991) found that plants with increased nectar production produced fewer seeds than control plants. Because plants in both treatments received supplemented pollination, the effect of increased resource allocation to the nectar was clearly seen to reduce the ability of high nectar-producing plants to mature seeds (Pyke 1991). In this study, fruit production was significantly lower on plants that were pollen supplemented, but exposed to robbery (more than 60% of these experimental flowers were robbed, pers. obs.), than on bagged and pollen supplemented plants (from xenogamy treatment). This suggests that increased fruit set levels in bagged flowers occurred as a consequence of energy saving from reduced nectar production. Note that bagged flowers produce a significantly lower nectar quantity than that produced by nectar-removed flowers (Navarro 1999).

Flowers of *Macleania bullata* possess the morphology and nectar characteristics of flowers adapted to pollination by long billed hummingbirds. However, this specialized system is very susceptible to nectar robbers against which morphological barriers do not exist. This study illustrates the necessity of delving deeply into the interactions between plants and their visitors (see Herrera 1996), as well as the need for a detailed understanding of the effect that nectar robbers have upon the fitness of typical long-billed hummingbird-pollinated flowers. Studies focused on the effect that nectar robbing has upon fitness of plants with hummingbird-pollinated flowers, will contribute to a better understanding of the complicate universe of animal-plant interactions.

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