

The Role of an Avian Nectar Robber and of Hummingbird Pollinators in the Reproduction of Two Plant Species

Author(s): M. C. Arizmendi, C. A. Dominguez and R. Dirzo

Source: *Functional Ecology*, Vol. 10, No. 1 (Feb., 1996), pp. 119-127

Published by: British Ecological Society

Stable URL: <http://www.jstor.org/stable/2390270>

Accessed: 11-10-2015 18:08 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Wiley and British Ecological Society are collaborating with JSTOR to digitize, preserve and extend access to *Functional Ecology*.

<http://www.jstor.org>

The role of an avian nectar robber and of Hummingbird pollinators in the reproduction of two plant species

M. C. ARIZMENDI, C. A. DOMÍNGUEZ AND R. DIRZO

Departamento de Ecología Evolutiva, Centro de Ecología UNAM, A.P. 70-275, México 04510 D.F., México

Summary

1. Flower nectar robbers which extract flower rewards to pollinators but do not pollinate, may reduce the fitness of the plant. In this study we combined field observations and experimental manipulations to assess the role of a primary nectar robber, the bird *Diglossa baritula*, on flower nectar secretion and reproductive output of two hummingbird-pollinated plant species with contrasting breeding systems. We used the hermaphroditic *Salvia mexicana* and the androdioecious *Fuchsia microphylla*. In addition, because the distinction between pollinators and robbers is not so sharp, we compared the pollination efficiencies of *D. baritula* and of five species of hummingbirds visiting the flowers of the same plant species.
2. Flowers of the two plant species were frequently robbed (92 and 37% of the flowers in *Salvia mexicana* and *Fuchsia microphylla* respectively). For both species, field censuses of robbed and unrobbed flowers showed no differences in fruit set. Experimentally induced nectar robbery did not affect the cumulative production of nectar in both plant species. However, in *S. mexicana*, but not in *F. microphylla*, intact flowers produced more concentrated nectar.
3. The role of *D. baritula* and hummingbirds on seed production per flower, was assessed by exposing individual flowers to different schedules of visitation by caged flower visitors. In *S. mexicana*, the number of seeds produced by flowers visited by the robber only was similar to that of flowers visited by the least efficient pollinator but lower than that of those visited by the other pollinators.
4. In *F. microphylla*, seed production by flowers visited by the robber only was lower than that of flowers visited by all other pollinators.
5. For both plant species visitation by the robber *plus* hummingbirds yielded a similar number of seeds as flowers visited by the more effective pollinator.
6. There was no field evidence that nectar robbery by *D. baritula* damages nectaries or ovules and, since under natural conditions flower visitation by the robber only was very rare, we conclude that for these two plant species *D. baritula* may be regarded as a commensal or even a low-efficiency pollinator.

Key-words: *Diglossa baritula*, *Fuchsia microphylla*, hummingbirds, nectar robbery, pollination efficiency, *Salvia mexicana*

Functional Ecology (1996) **10**, 119–127

Introduction

The effects of illegitimate flower visitors and nectar robbers on plant fitness are poorly documented (Inouye 1983; Roubik 1989). The effect can be positive if, by depleting nectar, robbers force pollinators to visit more flowers (Cushman & Beattie 1991), thus increasing outcrossing rates and seed production (Hawkins 1961; Heinrich & Raven 1972; Soberón & Martínez del Río 1985). Also, piercing of flowers by some bees may result in pollination as a result of

flower movement during the puncturing and robbery (Koeman-Kwak 1973; Roubik 1989). Negative effects of robbers on nectar and seed production are also known (McDade & Kinsman 1980; Roubik 1982; Roubik, Holbrook & Parra 1985), with bee nectar robbery being typically regarded as detrimental (see review in Roubik 1989). The effects of nectar robbers other than bees have been poorly studied and remain controversial. In spite of the common occurrence of nectar robbery by birds (Swynnerton 1916; Wolf, Stiles & Hainsworth 1976; Renner 1989; Willmer &

Corbet 1981; Eguiarte & Búrquez 1987), studies evaluating their effects on plant reproductive performance are scarce (see McDade & Kinsman 1980).

Legitimate visitors also vary in their efficiency as pollinators (thus affecting flower seed production; Schemske & Horvitz 1984; Campbell & Morten 1985; Herrera 1988; Cushman & Whitham 1989; Thompson & Pellmyr 1992) and the evolutionary relevance of such differential effectiveness of pollinators has been documented in several studies (Cruden 1972; Primack & Silander 1975; Schemske & Horvitz 1984; Montalvo & Ackerman 1986; Herrera 1987). It has been shown that differences in pollination efficiency relate to aspects such as the size of visitors (e.g. larger bees promote higher seed production than smaller ones in *Calathea ovandensis*; Schemske & Horvitz 1988) and climatic conditions that make some pollinators more efficient than others in visiting flowers (e.g. birds as compared to bees in high elevation sites; Cruden 1972). Also, the effect of a given species of pollinator can vary with respect to the presence and relative abundance of other species of visitors, the latter varying from robbers to true pollinators (Thompson & Pellmyr 1992). In turn, the interaction of plants with robbers and pollinators may be influenced by factors such as the morphology of the visitors, the plant's compatibility system, the availability and quality of rewards, and spatio-temporal variation in the abundance of flowers, robbers and pollinators (Schemske & Horvitz 1984; Herrera 1988; Horvitz & Schemske 1990; Cushman & Beattie 1991; Thompson & Pellmyr 1992). Given such complexity and interdependence of factors, the classification of floral visitors as either 'robbers' or 'pollinators' may be simplistic, as some robbers can act as pollinators (e.g. Hawkins 1961; Graves 1982) and pollinators can at times act as robbers (e.g. Schemske & Horvitz 1984; Roubik *et al.* 1985; Herrera 1988; Roubik 1989). Therefore, in order to assess the relative importance of pollinators and robbers on plant reproduction, detailed field observations and manipulations are needed.

The objective of this work was to evaluate the effect of the nectar robber *Diglossa baritula* Wagler (Passeriformes: Aves) on nectar secretion (accumulated volume and concentration) and seed set of two hummingbird-pollinated plant species, *Salvia mexicana* L. (Labiatae) and *Fuchsia microphylla* H.B.K. (Onagraceae). These plant species were selected because they were the most common hummingbird-pollinated plants at our study site and they share many species of flower visitors (both hummingbirds and *D. baritula*) (Arizmendi 1994). The nectar robber *D. baritula* feeds by holding the corolla tube with the hook-like upper mandible and piercing it with the shorter lower mandible. It then introduces its tongue which, by capillarity, extracts nectar (Skutch 1954). Because of the potential negative effect of this bird on plant reproduction, we aimed to answer the following questions: (1) is the number of flowers visited by hum-

mingbirds higher than that of *D. baritula*; (2) what is the frequency of nectar robbery under field conditions; (3) do flowers pierced by *D. baritula* produce less nectar and seeds than unrobbed flowers; (4) does the effect of *D. baritula* on plant reproduction change as a function of the identity and sequence of visits of the members of these plants' pollinator guild?

Materials and methods

STUDY AREA

Field work was conducted from November 1991 to February 1992, and from October 1992 to February 1993, at the Laboratorio Natural Las Joyas field station. This 1245 ha preserve is located in the Mexican States of Jalisco and Colima, in the Sierra de Manantlán (at 1952 m a.s.l.), about 50 km east of the Pacific coast (19° 35' N; 104° 16' W). Annual mean precipitation is 1610 mm, with most of it falling between June and October. Mean annual temperature is 14.6 °C, freezing temperatures occurring only for a few days during the winter. The vegetation is a complex mosaic of wet coniferous, pine-oak, and cloud forest, and secondary vegetation (Guzmán 1985; Saldaña-Acosta & Jardel 1991).

SPECIES STUDIED

At our study site, *D. baritula* is the main avian nectar robber of hummingbird-pollinated plants, taking nectar from 76% of the 21 species visited by hummingbirds (Arizmendi 1994). Twenty-one species of hummingbird have been recorded at Manantlán, thus making this site ideal for studies on plant-hummingbird-robber interactions.

Salvia mexicana is a self-compatible perennial herb. Its flowers are visited and pollinated by hummingbirds. Flowers are hermaphroditic with a long purple corolla tube (length, \bar{X} = 29.8; SD = 1.49 mm; n = 46); they last for 4 days and blooming is concentrated from November to March.

Fuchsia microphylla. Arroyo & Raven (1975) reported that, although this species superficially appears to be gynodioecious, among the plants they studied apparently hermaphrodite but female-sterile (functionally male) plants formed about 90% of the population; they described this system as subdioecious. At Manantlán we found this species to be a self-compatible androdioecious shrub (i.e. with male and hermaphrodite individuals). Male flowers lack gynoecium and are longer (\bar{X} = 12.03 ± 1.37 mm; n = 50) and brighter than the hermaphrodite ones (\bar{X} = 10.73 ± 1.26 mm; n = 50). The gender of the plants in the studied population has remained constant for three years, thus the bias from previous descriptions (see Arroyo & Raven 1975) does not appear to be owing to temporal variation in the sexual expression of this population. This contrast in sexual expression

warrants further study. Blooming of *F. microphylla* at Manantlán occurs throughout the year, with one peak from August to October and another from December to January. Individual flowers last for 5 days and are visited and pollinated by hummingbirds and bumblebees (Arizmendi 1994). Voucher specimens of both plant species are deposited in the ZEA herbarium.

FIELD PROCEDURES

Flower visitors

Direct observations of avian flower visitors were made in each of five patches of flowering plants for both plant species. Each patch was observed for 2 h during both peaks of daily bird activity (30 min after sunrise and 30 min before dusk, Arizmendi 1994). For each plant species, we selected those patches with high abundance of flowers. The whole area in that patch (never more than 3.5 m²) could easily be observed from a distance of 1–4 m. For each visit we recorded, for two consecutive days, the species of flower visitor and counted the number of flowers probed.

Frequency and position of damage on flowers in the field

The frequency of flowers damaged by nectar robbers was measured in 10 individuals of *S. mexicana* and 15 individuals of each sex of *F. microphylla*. For these plants, we counted the total number of damaged (i.e. pierced) and intact flowers per individual and, in the damaged flowers, the distance between the base of the flower and the hole made by the robber was measured. We also looked for the occurrence of damage to ovaries and stamens.

Effects of nectar robbery on fruit set under field conditions

Thirty plants of each species were randomly selected (only hermaphrodite plants of *F. microphylla* were used) and two last-day flowers, one robbed and one intact, were marked in each plant. After corolla withering, the calyx of each flower was bagged using a mosquito net-bag until fruit production. Fruit set (ratio fruits/flowers) was calculated for each flower type.

Effect of experimentally induced nectar robbery on nectar secretion

A sample of 140 first-day flowers of *S. mexicana* and 280 (140 male and 140 hermaphrodite) of *F. microphylla* was chosen at random from a total of 20 plants of *S. mexicana* and 10 plants of each sex of *F. microphylla*. Half of the flowers of each individual (chosen at random) were subjected to piercing by *D. baritula*, by holding one bird by the feet in front of

the flower and waiting until it pierced the corolla and extracted nectar. Flowers were then marked with thin plastic numbered rings. For each experimental flower, the presence of the characteristic hole produced by piercing was verified by visual inspection. Flowers lacking such a hole (e.g. incomplete robbery) were discarded. The unmanipulated flowers were marked and used as controls. After treatment, experimental and control flowers were covered with mosquito-net bags. Nectar was not removed from control flowers (as would be required for a thorough control) because the introduction of a micropipette results in damage of both the corolla and ovaries; this is undesirable because flower damage is the independent variable. One day after treatment, 10 flowers from each category were randomly selected every 2 h, from dawn to dusk, and the amount of nectar accumulated in each flower was measured with calibrated microcapillary tubes; sugar concentration was measured with a hand-held refractometer (ERMA 101190-32).

Effect of experimentally induced nectar robbery and pollination on seed set

We manipulated the order of visitation (robber or pollinator) and the species of hummingbird in experimental plants of both species. Hummingbirds belonged to the species most commonly observed visiting flowers of the focal plants. Except for *Selasphorus rufus*, all the birds used are resident at Manantlán. Thus, our experiments mimicked the composition of the avian pollinator guild these species are exposed to in the field.

For *S. mexicana* individually caged plants of similar size and captive birds belonging to four species of hummingbird and *D. baritula* were used. For each shrub, we marked each of eight randomly chosen flower buds with thin plastic numbered rings. At anthesis, each experimental flower within a plant was randomly assigned to one of eight pollination treatments. We measured the efficiency as pollinators (in terms of seed set) of each of four species of hummingbirds differing in bill size (*S. rufus* < *Hylocharis leucotis* < *Lampornis amethystinus* < *Eugenes fulgens*), and of *D. baritula*. Interactive effects were assessed by allowing one visit of *D. baritula* and one of *H. leucotis* (the most frequent flower visitor of both plant species), and then reversing the order. Finally, automatic self-pollination was assessed by bagging individual flowers with a fine cloth mesh to exclude both pollinators and robbers. We used 30 replicates per treatment (i.e. one flower per treatment on each of 30 plants).

Similar procedures were used with *F. microphylla* but the identity of hummingbirds was different. In this case we used only the common visitors *Atthis heloisa* and *H. leucotis*, and the piercer *D. baritula*. Interactive effects and automatic self-pollination were assessed as with *S. mexicana*. An additional treatment

of outcrossed hand pollination was used to establish the potentially maximum number of seeds this species can produce. We used 16 replicates per treatment (i.e. one flower per treatment on each of 16 plants).

Because there is no apomictic seed production in either of the studied species (Arizmendi 1994), we did not include a treatment with emasculated flowers.

Before anthesis, a mosquito-net cage (5×5×2 m) was placed over the target plant and two/three neighbouring conspecific shrubs. Flower buds of each treatment were bagged with a fine cloth-mesh. At anthesis, we unbagged one flower and the appropriate bird (according to treatment) was released into the cage and allowed to visit flowers. Only trials in which visits to the experimental flower occurred after visitation to flowers from the neighbouring conspecific plants were included in the sample. This procedure assured that birds visiting target flowers carried outcross pollen on their bodies. Once the target flower was visited, the bird was removed and the flower rebagged. Fruits from experimental flowers were later collected and the number of seeds per fruit counted.

Birds were captured at least 4 days before being used in the experiments and kept in individual cages. They were fed with a 20% solution of sugar offered in artificial feeders and fruit flies (*Drosophila* sp.) were provided *ad libitum*.

For each plant species, a pollination efficiency score (PES) was calculated for each species of bird as follows. Seed production per visit has been defined as the 'quality' component of pollination efficiency (Herrera 1987). This factor, multiplied by the 'quantity' component (i.e. the number of visits), defines the PES of a particular pollinator. We used the percentage of visited flowers from the field censuses as the quantity component (number of flowers visited by each bird species divided by total number of flowers visited by any pollinator) and the number of seeds produced per visit (from the above experiment) as the quality component. The PES compares relative pollination efficiencies of flower visitors and is not meant to be an estimate of the quality of seeds (progeny) produced.

Table 1. Species of birds visiting flowers (number and percentage) of *Salvia mexicana* (*S m*) and *Fuchsia microphylla* (*F m*) at Sierra de Manantlán, Jalisco

Bird species	Activity	Exposed culmen $\bar{X} \pm SD$	No. of visits		% flowers visited	
			<i>S m</i>	<i>F m</i>	<i>S m</i>	<i>F m</i>
<i>Amazilia beryllina</i>	Pollinator	20.1 ± 1.2	226	–	6.1	–
<i>Atthis heloisa</i>	Pollinator	13.5 ± 2.2	–	27	–	7.4
<i>Eugenes fulgens</i>	Pollinator	28.3 ± 1.0	11	–	0.3	–
<i>Hylocharis leucotis</i>	Pollinator	17.9 ± 0.8	1008	119	27.2	32.6
<i>Lampornis amethystinus</i>	Pollinator	21.7 ± 1.1	1263	–	34.1	–
<i>Selasphorus rufus</i>	Pollinator	17.7 ± 0.7	561	176	15.1	48.2
<i>Diglossa baritula</i>	Robber	–	637	42	17.2	11.6

For both plant species, the effects of among plant variation and pollination treatment on seed set were assessed using generalized linear models with a log link function (Baker & Nelder 1978, Healy 1988). Because the response variable consists of counts (number of seeds per treatment), error was declared as Poisson (Healy 1988).

Results

SALVIA MEXICANA

Flower visitors

This species was visited by five species of hummingbirds and by *D. baritula* (Table 1). All hummingbird species made legitimate visits to the flowers and therefore can be considered as potential pollinators. A single flower was observed to be repeatedly visited by hummingbirds, while nectar robbers visited only once (as indicated by direct observations and by the number of holes in the flowers). Out of 3706 observed visits, 637 (17%) were made by *D. baritula* and 3069 (83%) by hummingbirds. Thus, the ratio of the number of flowers visited by hummingbirds to those visited by robbers was 4.8.

Frequency and position of damage on flowers

A total of 92% of the surveyed flowers of *S. mexicana* were pierced by *D. baritula*. Piercing was done through the calyx at an average distance of 5.4 mm (SD = 2.2; $n = 46$) from the base of the flower, where the ovaries are located. Damage to the ovaries, styles or stamens was never detected.

Effects of nectar robbery on fruit set under field conditions

Robbed and intact flowers did not differ in their probability to set fruits under field conditions (fruit set = 0.80 and 0.66, for robbed and intact flowers respectively, $\chi^2_1 = 0.23$, $P > 0.50$). This result suggests again that ovaries are not damaged during nectar robbery.

Effect of experimentally induced nectar robbery on nectar secretion

The amount of accumulated nectar increased through time for both intact and robbed flowers ($F_{6,126} = 8.34$, $P < 0.05$, Fig. 1a). The pattern was very similar for both types of flower. In addition, the amount of nectar accumulated in robbed and intact flowers one day after robbery did not differ significantly ($F_{1,126} = 4.46$, $P > 0.10$). In contrast, nectar of intact flowers was significantly more concentrated than that of pierced flowers ($F_{1,126} = 38.14$, $P < 0.001$), although the difference is owing only to the last measurement of the day (Fig. 1b).

EFFECT OF EXPERIMENTALLY INDUCED NECTAR ROBBERY AND POLLINATION ON SEED SET

Seed production per flower among plants of *S. mexicana* did not differ significantly ($\chi^2_{29}=29.98$, $P>0.25$). In contrast, there were significant differences in seed production among pollination treatments ($\chi^2_7=102.52$, $P<0.001$). The interaction plant \times treatment was not significant ($\chi^2_{202}=195.4$, $P>0.1$). Automatic self-pollination was the treatment producing the lowest number of seeds (Table 2), and seed set of this treatment did not differ from that of visitation by *D. baritula*. Flowers visited by the robber produced a similar number of seeds as that of flowers visited by *E. fulgens* but it was lower than that of all other treatments (Table 2). With the exception of *H. leucotis* and *E. fulgens* (which yielded the lowest and highest seed sets, respectively), flowers pollinated by hummingbirds produced similar numbers of seeds (Table 2). The average number of seeds produced by flowers of *S. mexicana* under field conditions was 1.7 (Arizmendi

Table 2. Mean number of seeds produced by flowers of *Salvia mexicana* under different treatments of pollination ($n=30$). Means with the same letter are not significantly different (Tukey's test $P>0.05$)

Treatment	Mean	SD
Automatic self-pollination	0.1	0.4 ^a
<i>Diglossa baritula</i>	0.9	1.2 ^{ab}
<i>Eugenes fulgens</i>	1.4	1.3 ^{bc}
Pollination + <i>D. baritula</i>	1.7	1.3 ^{cd}
<i>Lampornis amethystinus</i>	1.9	1.3 ^{cd}
<i>D. baritula</i> + pollination	1.9	1.4 ^{cd}
<i>Selasphorus rufus</i>	2.2	1.3 ^{cd}
<i>Hylocharis leucotis</i>	2.5	1.2 ^d

1994), indicating that our experiment resembled natural levels of pollination.

Regarding pollination efficiency, *H. leucotis* and *L. amethystinus* yielded the highest values of PES (68.81 and 64.41, respectively). *S. rufus* was almost half as efficient (PES=33.67), and *E. fulgens* was the least efficient pollinator (PES=0.43). Unexpectedly, PES of the nectar robber was 30 times greater (15.91) than that of *E. fulgens*. This is owing largely to the quantitative component of PES.

FUCHSIA MICROPHYLLA

Flower visitors

Flowers of *F. microphylla* were visited by three species of hummingbirds, by *D. baritula* (Table 1) and by bumble bees (*Bombus* sp.). Both humming birds and bumble bees made legitimate visits and, again, flowers of this species, were robbed only once. The ratio of the number of flowers visited by hummingbirds/*D. baritula* was 8.6 (365:42). Although male and hermaphrodite flowers received almost the same number of visits (male 185, hermaphrodite 180), hermaphrodite flowers were robbed significantly less often ($\chi^2_1=20.65$, $P<0.001$). In male flowers the ratio of the number of flowers visited by hummingbirds/robbers was 4.7 (185:39) while in hermaphrodite flowers the ratio was 20 (180:9).

Frequency and position of damage on flowers in the field

Holes were made at the bases of the corolla tubes (mean distance from ovaries in hermaphrodite flowers =3.2 mm, SD=0.2, $n=50$), and were present in 26% of the hermaphrodite and 43% of the male flowers (299 flowers in 15 male and 189 flowers in 15 hermaphrodite plants). Damage to the ovary was never detected in hermaphrodite flowers. Likewise, evidence of damage to stamens was not detected.

Effects of nectar robbery on fruit set under field conditions

Under natural conditions the fruit sets of robbed and unrobbed hermaphrodite flowers were 0.87 and 0.63

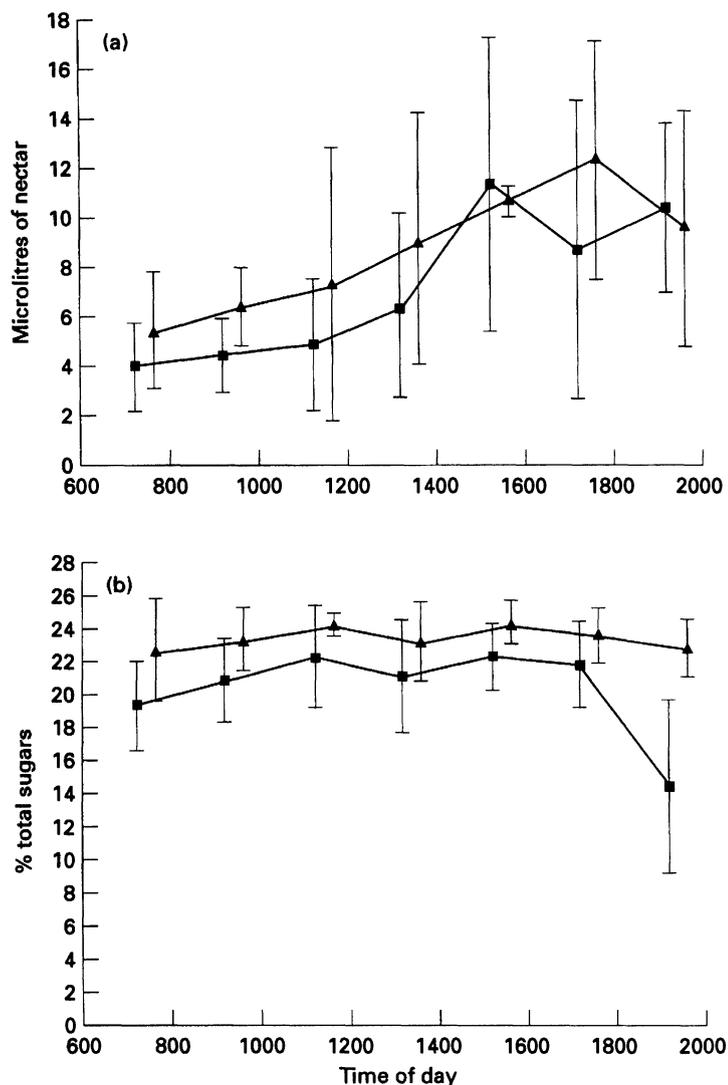


Fig. 1. Nectar volume and concentration in intact (▲) and robbed (■) flowers of *Salvia mexicana*. (a) Nectar volume; (b) nectar concentration. Data are means \pm ISD ($n=10$). Data on the x-axis are slightly displaced for clarity.

respectively ($\chi^2_1=0.61$, $P>0.50$), indicating that no damage occurred to the ovaries.

Effects of experimentally induced nectar robbery on nectar secretion

Nectar robbery did not affect significantly either nectar quantity ($F_{1,262}=0.14$, $P>0.05$) or concentration ($F_{1,262}=3.91$, $P>0.05$). In contrast, male flowers produced more nectar ($F_{1,262}=23.61$, $P<0.001$) and with higher sugar concentration ($F_{1,262}=29.41$, $P<0.001$) than the hermaphrodite ones (Fig. 2). There were no significant differences through time either in nectar volume ($F_{6,262}=1.41$, $P>0.05$) or concentration ($F_{6,262}=1.21$, $P>0.05$). Interactions among factors were not significant ($P>0.1$ in all cases).

Effect of experimentally induced nectar robbery and pollination on seed set

Seed production per flower among plants did not differ significantly ($\chi^2_{15}=13.6$, $P>0.05$). In contrast, there were significant differences in seed production among pollination treatments ($\chi^2_6=675.4$, $P<0.001$). The interaction plant \times treatment was also significant ($\chi^2_{89}=300.8$, $P<0.001$). Visitation by only *D. baritula* produced the lowest seed set of all treatments

(Table 3). Automatic self-pollination also produced a significantly lower number of seeds than treatments involving hummingbird visitation and manual outcrossing pollination. Seed set did not vary with hummingbird species (Table 3). Manual outcrossing pollination was the treatment producing significantly more seeds than all other treatments but *H. leucotis* and *H. leucotis*+*D. baritula*. These results indicate that the potentially negative effect of *D. baritula* on seed production of *F. microphylla* depends on the likelihood that individual flowers will be visited only by nectar robbers.

Pollination efficiency scores for the avian flower visitors of *F. microphylla* indicate that *H. leucotis* was five times more efficient (PES=538.56) than *A. heloisa* (PES=98.25). The PES of *D. baritula* (1.74) was 56 times lower than that of the least efficient hummingbird (*A. heloisa*).

Discussion

We found that both *S. mexicana* and *F. microphylla* experience considerable nectar robbery by *D. baritula*. The levels of robbery however, do not seem to affect fruit production under field conditions. Our experimental manipulations showed that nectar production by robbed and intact flowers was statistically

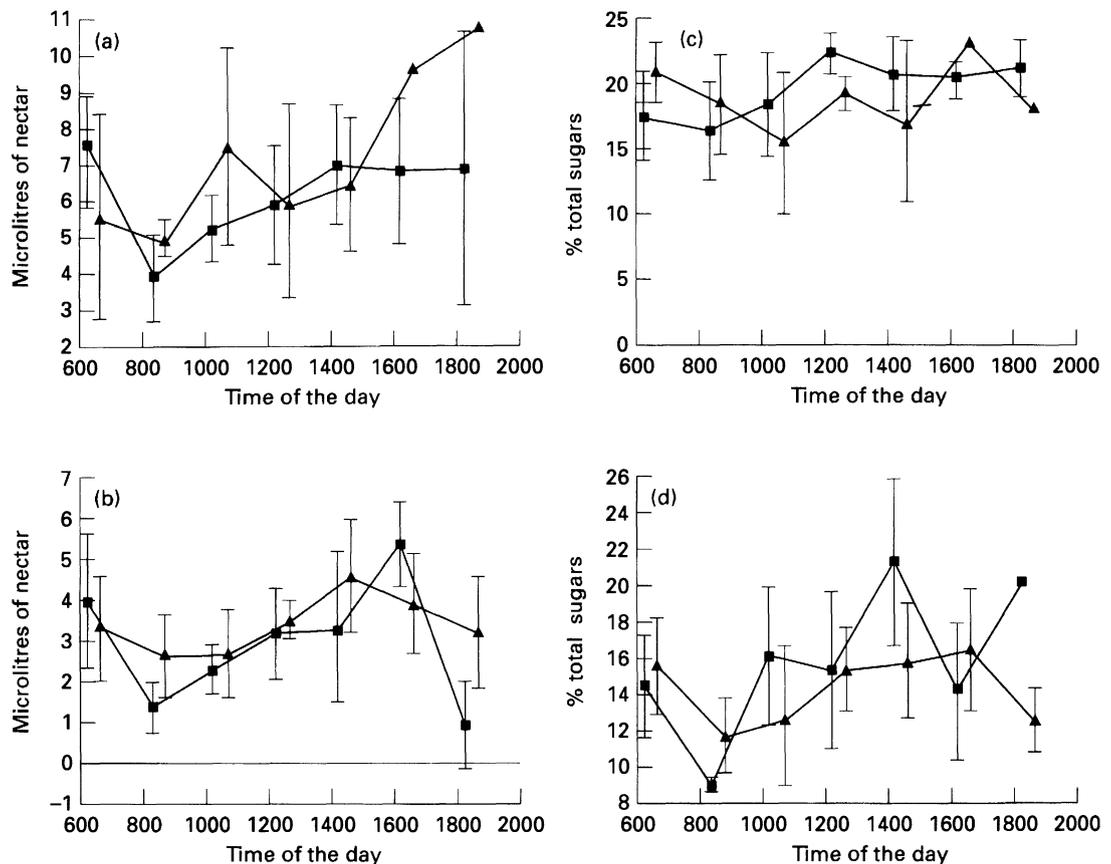


Fig. 2. Nectar parameters in intact (▲) and robbed (■) flowers of *Fuchsia microphylla*. Nectar volume in male (a) and hermaphrodite (b) flowers; nectar concentration in male (c) and hermaphrodite (d) flowers. Data are means \pm ISD ($n=10$). Data on the x-axis are slightly displaced for clarity.

Table 3. Mean number of seeds produced by flowers of *Fuchsia microphylla* under different treatments of pollination ($n=16$). Means with the same letter are not significantly different (Tukey's test $P>0.05$)

Treatment	Mean	SD
<i>Diglossa baritula</i>	0.2	0.5 ^a
Automatic self-pollination	4.6	7.2 ^b
<i>Atthis heloisa</i>	13.1	10.8 ^c
<i>D. baritula</i> + Pollination	13.6	11.5 ^c
Pollination + <i>D. baritula</i>	15.9	10.1 ^{cd}
<i>Hylocharis leucotis</i>	16.5	9.5 ^{cd}
Outercross pollination	19.2	8.7 ^d

indistinguishable in both plant species. This lack of difference suggests that, although robbed flowers had to invest more to compensate for the nectar consumed by the robber, no damage to secretory tissues occurred. However, nectar concentration of *S. mexicana* was affected by nectar robbery: damaged flowers produced more diluted nectar than undamaged ones. This dilution could be a plant's response to invest less in already-robbed flowers. For example, nectar amino acid and sugar content have been shown to be reduced by robbing by bees (Roubik 1989). Our results also suggest that the consequences of producing a less concentrated nectar are negligible (see below). On the other hand, the experiments showed that the effect of *D. baritula* on the reproductive output of the two plant species varied depending on the plant species and on the presence of other flower visitors.

Both field observations and experimental evidence showed that the activities of *D. baritula* on *S. mexicana* flowers had no negative effect on the plants' reproductive output and that this visitor may even act as a low-efficiency pollinator.

The single negative effect on seed production found in this study occurred in those experiments where *D. baritula* was the only visitor of *F. microphylla* flowers. Here, seed production was reduced 30-fold with respect to automatic self-pollination. This result contrasts with field observations where no differences in fruit set between robbed and intact flowers were found. Two lines of evidence could resolve this apparent contradiction. First, at our study site hummingbirds greatly outnumbered nectar robbers and thus a robbed flower has a high probability of being visited by hummingbirds (see also Arizmendi 1994). Second, there were no differences in seed production among treatments involving visits by hummingbirds plus *D. baritula* (see Table 3). Therefore, although visits by *D. baritula* alone would reduce seed production in *F. microphylla*, this condition would rarely be met in the field owing to visits by other pollinators.

Our data demonstrate that the effect of *D. baritula* on the reproductive success of the studied species may range from that of low-efficiency pollination to almost neutrality. This underscores the necessity of

studying the effect of each flower visitor separately on different plant species (Horvitz & Schemske 1984; Schemske & Horvitz 1984; Herrera 1988), and on different ecological contexts. As this and other studies (e.g. Thompson & Pellmyr 1992) show, the role of a given flower visitor can range from unidirectional exploitation (*sensu* Dafni 1984) to mutualism depending on the presence of other flower visitors.

The efficiency of hummingbirds as pollinators of *S. mexicana* was variable and related to bill length. *E. fulgens*, the species with the longest bill was the poorest pollinator, with an efficiency similar to that of *D. baritula*. Although *S. mexicana* can produce seeds in the absence of pollinators, pollinator-visited flowers produced more seeds than unvisited ones. Hummingbirds with the shortest bills were associated to the highest seed production per flower. *Hylocharis leucotis* and *S. rufus* have an exposed culmen of around 17 mm each, while the average length of the corolla is 29.83 mm (SD=2.4). Therefore, during their visits, these birds' foreheads effectively contact the anthers of the flowers as they force themselves to reach for nectar. Pollination by the largest hummingbird, *E. fulgens*, produced significantly fewer seeds per flower than by *H. leucotis*. The exposed culmen of *E. fulgens* is around 28 mm (SD=0.9), which together with the length of the tongue (Johnsgard 1983), becomes almost twice as long as the corolla tube of *S. mexicana*. This means that pollen of *S. mexicana* is deposited on the bill rather than in the forehead (M. C. Arizmendi, personal observations). Hummingbird bills are covered by a waxy substance (Johnsgard 1983) and as a result pollen falls off easily and quickly, thus reducing the likelihood of effective pollen transfer. Pollination by *L. amethystinus*, the hummingbird of medium-size bill, showed no differences in seed production with respect to either the smaller or the larger ones.

In contrast to *S. mexicana*, in *F. microphylla* all the treatments involving visitation by hummingbirds produced similar numbers of seeds. This result could be a consequence of the reduced variance in bill length among the flower visitors of *F. microphylla* when compared to those of *S. mexicana* ($s^2=6.9$ and 16.5 visitors of *F. microphylla* and *S. mexicana*, respectively; variances comparison: $F_{49,29}=2.38$, $P<0.002$).

As stated by Schemske & Horvitz (1984), variation among pollinators in their ability to promote seed production is a plant's precondition for the evolution of pollinator specialization. This ability, in turn, depends on both the 'quality' and 'quantity' components of pollination efficiency (Herrera 1987). In this view, *H. leucotis* was the most efficient pollinator of both plant species. This hummingbird's efficiency was 160 and 309 times greater than that of the least efficient flower visitors of *S. mexicana* and *F. microphylla*, respectively. As showed by our results, there is enough variation in the ability of pollinators to produce seeds, thus the assumed preconditions that could favour pol-

linator specialization are met for both plant species. This suggestion contrasts with the generally held view of hummingbird-pollinated plants as visited by a diverse array of species and therefore lacking specialized pollinators (i.e. Feinsinger 1976, 1978; Wolf, Stiles & Hainsworth 1976; Stiles 1980; Jordano 1987). The lack of specialization in hummingbird-pollinated plants so far studied could have at least three explanations: (1) from the plant's perspective, all flower visitors are equivalent in terms of their pollination efficiency; (2) natural selection for pollinator specialization is underway and we are witnessing an unfinished, ongoing process; (3) the specific composition of the pollinator guild varies through time and space, leading to a spatio-temporal shift in the rank of the different hummingbird species' pollination efficiency. Our results clearly do not concur with the first of the three explanations, yet they do not allow us to distinguish between the other two alternatives. Nonetheless, given the ubiquitous variation in specific composition and abundance of hummingbird pollinators in time and space (Feinsinger & Colwell 1978; Arizmendi & Ornelas 1990; Arizmendi 1994), specialization in plant hummingbird pollination systems in nature may represent an exception rather than a rule.

Acknowledgements

We wish to thank L. Domínguez, E. Vega and L. González for their help during field work. We thank V. Sánchez, E. Jardel and all the staff of the Estación Científica Las Joyas for facilities given. Comments by L. Eguiarte, J. Núñez-Farfán, C. Macías-García, H. Drummond, G. Stiles, N. Waser, D. W. Roubik and A. Dafni, greatly improved an earlier draft of this paper. This research was supported by a DGAPA grant (IN208991-UNAM to R. D.) and by a CONACYT doctoral fellowship (48277 to M.C. A.).

References

- Arizmendi, M.C. (1994) *Interacciones ecológicas múltiples: el caso de la polinización por colibríes y el ladrón de néctar Diglossa baritula*. PhD thesis, Centro de Ecología, UNAM, Mexico.
- Arizmendi, M. C. & Ornelas, J. F. (1990) Hummingbirds and their floral resources in a tropical dry forest in Mexico. *Biotropica* **22**, 172–180.
- Arroyo, M.T.K. & Raven, P.H. (1975) The evolution of subdioecy in morphologically gynodioecious species of *Fuchsia* sect. *Encliandra* (Onagraceae). *Evolution* **29**, 500–511.
- Baker, R.J. & Nelder, J.A. (1978) *The Glim System Release 3. Generalized Linear Interactive Modelling*. Royal Statistical Society, Oxford.
- Campbell, D.R. & Morten, A.F. (1985) The mechanism of competition for pollination between two forest herbs. *Ecology* **66**, 554–563.
- Cruden, R.W. (1972) Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. *Science* **170**, 1439–1440.
- Cushman, J.H. & Whitham, T.G. (1989) Conditional mutualism in a membracid-ant association: temporal, age-specific and density-dependent effects. *Ecology* **70**, 1040–1047.
- Cushman, J.H. & Beattie, A.J. (1991) Mutualisms: assessing the benefits to hosts and visitors. *Trends in Ecology and Evolution* **6**, 191–195.
- Dafni, A. (1984) Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* **15**, 259–278.
- Eguiarte, L. & Búrquez, A. (1987) Reproductive ecology of *Manfreda brachystachya*, an iteroparous species of Agavaceae. *Southwestern Naturalist* **32**, 169–178.
- Feinsinger, P. (1976) The organization of a tropical guild of nectarivorous birds. *Ecological Monographs* **46**, 257–291.
- Feinsinger, P. & Colwell, R.K. (1978) Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs* **48**, 269–287.
- Graves, G.R. (1982) Pollination of *Tristerix* mistletoe (Loranthaceae) by *Diglossa* (Aves, Thraupidae). *Biotropica* **14**, 316.
- Guzmán, M.R. (1985) Reserva de la Biósfera de la Sierra de Manantlán, Jalisco: Estudio descriptivo. *Tiempos de Ciencia* **1**, 10–26.
- Hawkins, R.P. (1961) Observations on the pollination of red clover by bees. I. The yield of seeds in relation to the numbers and kinds of pollinators. *Annals of Applied Biology* **49**, 55–65.
- Healy, M.J.R. (1988) *GLIM an Introduction*. Oxford Science Publications. Oxford University Press, Oxford.
- Heinrich, B. & Raven, P.H. (1972) Energetics and pollination ecology. *Science* **176**, 597–602.
- Herrera, C.M. (1987) Components of the 'quality' component: comparative analysis of a diverse insect assemblage. *Oikos* **50**, 79–90.
- Herrera, C.M. (1988) Variations in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* **35**, 95–125.
- Horvitz, C.C. & Schemske, D.W. (1984) Effects of an anted herbivore on seed production of a neotropical herb. *Ecology* **65**, 1369–1378.
- Horvitz, C.C. & Schemske, D.W. (1990) Spatio temporal variation in insect mutualism of a neotropical herb. *Ecology* **71**, 1085–1097.
- Inouye, D.W. (1983) The ecology of nectar robbing. *The Biology of Nectaries* (eds T. S. Elias & B. Bentley), pp 152–173. Columbia University Press, New York.
- Johnsgard, P.A. (1983) *The Hummingbirds of North America*. Smithsonian Institution Press, Washington, DC.
- Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries and coevolution. *The American Naturalist* **126**, 657–677.
- Koeman-Kwak, M. (1973) The pollination of *Pedicularis palustris* by nectar thieves (short-tongued bumblebees) *Acta Botanica Neerlandica* **2**, 608–615.
- McDade, L.A. & Kinsman, S. (1980) The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. *Evolution* **34**, 944–958.
- Montalvo, A.M. & Ackerman, J.D. (1986) Relative pollinator effectiveness and evolution of floral traits of *Spathyphyllum friedrichsthalli* (Araceae). *American Journal of Botany* **73**, 1665–1676.
- Primack, R.B. & Silander, J.A. (1975) Measuring the relative importance of different pollinators to plants. *Nature* **255**, 143–144.
- Renner, S.S. (1989) Floral biological observations on *Heliamphora tatei* (Sarracenaceae) and other plants from Cerro de la Neblina in Venezuela. *Plant Systematics and Evolution* **163**, 21–29.

- Roubik, D.W. (1982) The ecological impact of nectar robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* **63**, 354–360.
- Roubik, D.W. (1989) *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge.
- Roubik, D.W., Holbrook, N.M. & Parra, G. (1985) Roles of nectar robbers in the reproduction of a tropical treelet, *Quassia amara* (Simaroubaceae). *Oecologia* **66**, 161–167.
- Saldaña-Acosta, A. & Jardel, E.J. (1991) Regeneración natural del estrato arbóreo en bosques subtropicales de montaña en la Sierra de Manantlán, México: estudios preliminares. *Biotam* **3**, 36–50.
- Schemske, D.W. & Horvitz, C.C. (1984) Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* **225**, 519–521.
- Schemske, D.W. & Horvitz, C.C. (1988) Plant–animal interactions and fruit production in a neotropical herb: a path analysis. *Evolution* **69**, 1128–1137.
- Skutch, A. F. (1954) *Life Histories of Central American Birds*, vol. I. *Pacific Coast Avifauna Series* 31. University of California, Berkeley, CA.
- Soberón, J. & Martínez del Río, C. (1985) Cheating and taking advantage. *The Biology of Mutualism: Ecology and Evolution* (ed. D. Boucher), pp 192–213. Oxford University Press, New York.
- Stiles, F.G. (1980) Ecological and evolutionary implications of hummingbird pollination. *American Zoologist* **18**, 715–727.
- Swynnerton, C.F.M. (1916) Shortcuts by birds to nectaries. *Journal of the Linnean Society (Bot)* **43**, 381–518.
- Thompson, J.N. & Pellmyr, O. (1992) Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. *Ecology* **73**, 1780–1791.
- Willmer, P.G. & Corbet, S.A. (1981) Temporal and microclimatic partitioning of the floral resources of *Justicia aurea* a concourse of pollen vectors and nectar robbers. *Oecologia* **51**, 67–78.
- Wolf, L.L., Stiles, F.G. & Hainsworth, F.R. (1976) Ecological organization of a tropical highland hummingbird community. *Journal of Animal Ecology* **22**, 155–159.

Received 8 November 1994; revised 13 September 1995; accepted 13 October 1995