

---

# AVIAN NECTAR ROBBERS OF *Passiflora mixta* (Passifloraceae): DO THEY HAVE A POSITIVE EFFECT ON THE PLANT?

ROXIBELL C. PELAYO, CARLOS RENGIFO  
and PASCUAL J. SORIANO

---

## SUMMARY

The effect of nectar robbing on plant reproduction may be negative, positive or neutral. The effect was evaluated on *Passiflora mixta*, an Andean high-mountain species that is pollinated by the Sword-billed Hummingbird (*Ensifera ensifera*). We determined: 1) the bird assemblage associated with *P. mixta* flowers, 2) the *P. mixta* flower nectar production pattern, 3) how nectar robbing affects fruit and seed production and 4) self-incompatibility in this species. Eight bird species were found associated with *P. mixta* flowers: five hummingbirds, two flower-piercers and one oriole. Experiments support the plant self-incompatibility. Nectar robbers do not harm the plant reproductive structure. The effect of nectar robbing appears to be positive, since robbers diminish the resource offered increasing pollen flow. In consequence, the effect of nectar robbers on *P. mixta* could be considered a relation of indirect mutualism

lant-pollinator interactions may be affected by animals that exhibit a type of behavior called cheating; that is, they obtain the reward involved in a mutualistic interaction without providing the corresponding pollination service (Tyre and Addicott, 1993; Addicott and Tyre, 1995; Morris, 1996). Examples of this behavior are the so called nectar robbers, which can be a bird, an insect or another animal capable of extracting nectar from flowers through an opening made in the base of the corolla. This type of illegitimate visit is classified as primary, if they perforate the corolla, and secondary, if they take advantage of holes made by other robbers (Inouye, 1980; Irwin, 2000; Maloof and Inouye, 2000). Additionally, this type of interaction can affect the abundance of nectar available to the legiti-

mate pollinator (Irwin and Brody, 1998; Maloof and Inouye, 2000). Nectar robbers may not always exhibit this behavior if they are able to act as legitimate visitors to the flowers of other plant species. However, they show a preference for flowers with corollas that are long and/or produce large amounts of nectar (Maloof and Inouye, 2000; Lara and Ornelas, 2001).

Sword-billed Hummingbird usually act as nectar robbers on flowers with long corollas, while all the species of the genera *Diglossa* and *Diglossopsis* (Thraupidae), so-called flower-piercers, exhibit this behavior. Some Psittacidae, Fringillidae and other Thraupidae also engage in this behavior (Lyon and Chadek, 1971; Graves, 1982; Roubik *et al.*, 1985; Arizmendi *et al.*, 1996; Traveset *et al.*, 1998; Isler and Isler, 1999; Cotton, 2001; Lara and Ornelas, 2001; Navarro, 2001).

It is known that nectar robbing can be positive, negative or neutral, and can exert a selection pressure on flower morphology and plant-pollinator interactions (Arizmendi *et al.*, 1996; Traveset *et al.*, 1998; Maloof and Inouye, 2000; Irwin *et al.*, 2001; Lara and Ornelas, 2001; Navarro, 2001; Kjonaas and Rengifo, 2006). In the majority of papers indicating that nectar robbing diminishes the plant's fitness; the effective pollinator is a hummingbird, which suggests that the systems mentioned could be the most susceptible ones to affected by this phenomenon.

The passion flower *Passiflora mixta* L. (Passifloraceae) is distributed from Venezuela to Bolivia, from 1700 to 3700masl. Its exclusive pollinator is the Sword-billed Hummingbird (*Ensifera ensifera* Boissoneau), which is the only species that makes legitimate

---

**KEYWORDS** / Andes / *Ensifera ensifera* / Hummingbird / Nectar Robbers / Venezuela /

Received: 06/05/2010. Modified: 05/06/2011. Accepted: 05/08/2011.

**Roxibell C. Pelayo.** Biologist and M.Sc. in Tropical Ecology, Instituto de Ciencias Ambientales y Ecológicas (ICAE), Universidad de Los Andes (ULA), Venezuela. Professor, ULA, Venezuela. e-mail: roxibell@ula.ve

**Carlos Rengifo.** Biologist and M.Sc. in Tropical Ecology, ICAE-ULA, Venezuela. Director, Ornithological Station La Mucuy, Nacional Park Sierra Nevada, Mérida, Venezuela.

**Pascual J. Soriano.** Biologist, M.Sc. and Doctor in Tropical Ecology, ICAE-ULA, Venezuela. Professor, ULA, Venezuela.

---

visits to its flowers (Escobar, 1988; Lindberg and Olesen, 2001). The two species have a similar geographical distribution suggesting a co-evolutionary process (Snow and Snow, 1980; Lindberg and Olesen, 2001).

We deem important to evaluate the effect of nectar robbing on *P. mixta*, a plant that belongs to a pollinator system restricted to the high Andean mountains, involving a hummingbird species as the effective pollinator and could be negatively affected by nectar robbing. Hence, the general objective was to study the effect of nectar robbing on the plant-pollinator interaction and *P. mixta* fitness. Specific objectives included: 1) to determine the bird assemblage associated with *P. mixta* flowers, 2) to determine the *P. mixta* flower nectar production pattern, 3) to evaluate how nectar robbing affects fruit and seed production, and 4) to evaluate self-incompatibility in this plant species.

## Methods

### Study site

Fieldwork was carried out in El Rincón de la Venta, a locality in the middle basin of the Motatán River, 10km south-west of Timotes, Mérida State, Venezuela (8°54'38"N, 70°46'46"W), at an altitude of 2900m. The site occupies a dry slope on the limits between the Andean páramo and high-mountain dry evergreen forest ecological units (Ataroff and Sarmiento, 2003). Temperature follows an isothermal pattern with a yearly average of 10.2°C, while annual precipitation averages 1065mm, with a bimodal distribution and peaks in February and June. The site exhibits a significant degree of anthropic alteration produced by the expansion of the agricultural frontier, where, besides *Passiflora mixta*, species of the *Espeletia*, *Baccharis*, *Vaccinium*, *Echeveria*, *Lupinus*, *Psammisia* and *Fuchsia* genera predominate.

### *Passiflora mixta*

*P. mixta* is a climbing and long-lived perennial plant, with angular striated stems and trilobulate leaves with serrated borders. Flowers are long tubular (135mm), erect or horizontal, with cylindrical green hypanthia that turn pink toward the apex, pink/yellow colored sepals; petals subequal to the sepals, corona in a series, usually purple. It flowers and yields fruit throughout the year, and it has been suggested that it is self-incompatible (Escobar, 1988; Lindberg and Olesen, 2001).

### *Ensifera ensifera*

The Sword-billed Hummingbird *E. ensifera* is a traplinner species weighing 12g and has a body length of 140mm. It has an unusually long bill (102mm males, 114mm females) bent slightly upwards (Garrison and Gass, 1999; Gutiérrez *et al.*, 2004a, b; Hilty, 2003).

### Assemblage of birds associated with *P. mixta* flowers

Along the border of the Motatán River, 12 patches 1 to 50m<sup>2</sup> of *P. mixta* were selected, physically separated from 10 to 200m. Between March-June 2005 and March-April 2006, the avian visitors (36-175 flowers), were recorded using binoculars (10×40) during 1h observation cycles (0630-1900h) for a total observation time of 120h. As the number of flowers varied according to time and site, the total effort was 12750h/flower. Bird species were identified using the Venezuelan bird guide (Hilty, 2003) and the type of visit (legitimate or nectar robbing) was recorded. Nectar robbing species were classified as primary robbers and secondary robbers. Likewise, for each species, the cumulative visit frequency was calculated, standardizing the data for 1000 flowers per time interval. The variation throughout the day. The EstimateS program was used to generate rarefaction curves with the Mao Tao indices and the Chao 2 and Jackknife 1 richness indices (Colwell, 2005) were calculated. Finally, we determined the differences of the bird species visit frequency by means of a chi-square and standardized residuals test (Zar, 1999).

### Nectar production pattern: volume-concentration

Volume and concentration of the nectar produced during the period between anthesis and wilting (3 days) was calculated for each flower. For this purpose, a hole was made in the base of the hypanthium using a 100µl capillary tube; immediately thereafter, as many as 20µl capillary tubes as necessary to extract all the nectar found in the nectar chamber were introduced, measuring the length of the nectar column in the capillary tubes to determine the volume. This procedure was repeated at 1h intervals between 06:30 and 18:30. Using a field refractometer (Eclipse, Bellingham+Stanley), the sugar concentration in each of the samples was determined. In order to obtain the nectar production patterns from each flower, the same flowers were measured from the time that they opened until they closed. To prevent robbing and legitimate visits before and during anthesis

on the flowers used for measurements (n=14), part of the hypanthium was covered with acetate rings, including the area where the nectary is found internally, and each flower was isolated in a veil bag.

Analysis of variance for repeated measurements on the volume and concentration data was performed (p<0.05) in order to determine differences among the anthesis days and/or among the flowers measured. Additionally, in order to test if avian visits were associated with volume or nectar concentration, Spearman correlations between the average nectar volumes produced on the second day, the third day and the average for both days, and the activity patterns of each bird species were carried out. In these analyses, the first day of anthesis was not considered because nectar production was very low during that day.

### Reproductive biology

Between September 2005 and January 2006 the breeding system of the flowers was determined through a field experiment consisting of three treatments:

- 1) Autogamy (n=16): un-opened flowers were selected and covered with veil bags that prevented the access of any visitor. Simultaneously, the flowers were fertilized manually, with their own pollen, as they are herkogamies (anthers are 8-10mm below the stigma).
- 2) Xenogamy (n=9): un-opened flowers were emasculated before the anthers reached maturity. Manual pollination was performed with pollen from different and spatially distant (>20-50m) individuals.
- 3) Controls (n=14): flowers exposed to pollinator visits.

All three treatments were carried out simultaneously on flowers belonging to the same patch. For manual fertilization, an artist's paintbrush was used and washed with distilled water after each pollen application. Pollination was performed twice a day (morning and afternoon) from the day of anthesis until the flowers wilted. Stigmatic receptivity tests in different flowers (n=57) were carried out by determining peroxidase enzyme activity, submerging the stigmas in 3% hydrogen peroxide at different times of the day in the three anthesis days (Kearns and Inouye, 1993); these flowers were not used in the breeding system experiments.

All the flowers were protected from nectar robbing by placing acetate rings over the nectary. Each of the flowers in the three treatments were labeled with colored tape, placed under the stipules of the pedicel base, so that the abscission scar could be detected in case of abortion.

In all cases, the flowers were monitored until fruit production and the number of seeds in each one was counted.

Two circumstances significantly limited the number of replicates in the three treatments: the low number of open flowers on their first day of anthesis, so as to conduct all the treatments simultaneously, and the fact that a high number of the used flowers were destroyed by slugs.

#### Effect of nectar robbing on reproductive activity of the plant

The procedure for measuring and comparing fruit and seed production during low and high florescence intervals was as follows. From September-December 2005 (low florescence interval; 0-35 flowers) 31 robbed and 31 unrobbed flowers were selected, and from March-September 2006 (high florescence interval; 4-180 flowers) 45 robbed and 56 unrobbed flowers were selected, all belonging to the same patches used during the observations of avian flower visitors. Excluders (acetate rings on the base of the hypanthium) were placed on the unrobbed flowers to prevent nectar robbing while permitting legitimate flower visits. Robbed flowers were not manipulated. Finally, fruit seed sets were counted.

#### Damage to floral structures by nectar robbers

In order to determine whether the robbers caused any damage to the reproductive organs (ovaries, stigmas, anthers or androgynophore), 54 robbed flowers were randomly selected to compare their reproductive structures with those that remained intact (n=20).

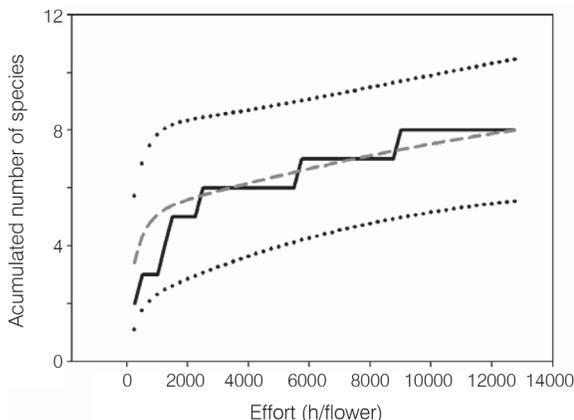


Figure 1. Accumulation curves (solid line) and rarefaction (dashed line) for birds associated with *Passiflora mixta* flowers and their confidence interval (dotted lines). Mao Tao index.

TABLE I  
BIRD SPECIES ASSOCIATED WITH  
*Passiflora mixta* FLOWERS

Species	NR1	NR2	LV
<i>Heliangelus mavors</i> (Trochilidae)	+	+	-
<i>Metallura tyrianthina</i> (Trochilidae)	-	+	-
<i>Coeligena eos</i> (Trochilidae)	-	+	-
<i>Colibri coruscans</i> (Trochilidae)	-	+	-
<i>Diglossa gloriosa</i> (Thraupidae)	+	+	-
<i>Diglossa sittoides</i> (Thraupidae)	+	+	-
<i>Icterus chrysater</i> (Icteridae)	+	-	-
<i>Ensifera ensifera</i> (Trochilidae)	-	-	+

NR1: primary nectar robbers, NR2: secondary nectar robbers, LV: legitimate visitor. The + and - signs indicate, respectively, that the bird exhibits positive or negative behavior for the type of interaction taken into consideration.

## Results

### Avian assemblage and other animals associated with *P. mixta*

Eight bird species were found associated with *P. mixta* flowers (Table I). *Hemispingus superciliaris* (Thraupidae) was also recorded at the study site outside the observation periods, as well as *Heliangelus spencei* and *Diglossa albilatera* near the study site. The species accumulation curve reached saturation with eight species; however, the rarefaction model predicted the possibility of a pair of additional species (Figure 1). Likewise, the Chao 2 and Jackknife 1 richness indices estimated a number of species slightly greater than found (8.49 and 9.96, respectively). Nevertheless, our empirical data are located on the lower limit of the Chao 2 richness estimator confidence interval (Figure 1).

Of all the species recorded, *E. ensifera* was the only one that always made legitimate visits, while the rest of the visitors were nectar robbers. Only *D. gloriosa*, *D. sittoides*, *H. superciliaris*, *I. chrysater*, and rarely *H. mavors* were primary robbers, while the rest of the hummingbirds did so as secondary robbers. When the flower had been previously perforated, *D. gloriosa* and *H. mavors* acted as secondary robbers. No nectar robbers were observed coming into contact with flower reproductive structures.

*Diglossa gloriosa* and *H. mavors* exhibited territorial behavior, aggressively defending the patches from their own and other species. *Diglossa gloriosa* displaced *H. mavors* and other hummingbirds, while *H. mavors* did so with the rest of the hummingbirds, with the exception of

*E. ensifera*. As far as *E. ensifera* is concerned, it never showed aggressive behavior nor was it displaced by any other bird species.

All the short-billed hummingbird species that acted as nectar robbers on *P. mixta* visited legitimately the flowers of *Fuchsia* spp. (Onagraceae), *Psammisia* sp. (Ericaceae) and *Salvia* sp. (Lamiaceae). Insects were also observed in association with *P. mixta* flowers, the most conspicuous being bumblebees that act as primary robbers, beetles as secondary robbers and pollen consumers, as well as bees that robbed nectar.

*E. ensifera* showed two activity peaks, one in the morning and the other in the afternoon; however, the most frequent robbers (*D. gloriosa* and *H. mavors*) made significant use of the resource throughout the day. On the other hand, *M. tyrianthina* showed a visiting behavior similar to that of *E. ensifera*, while the rest of the nectar robbers showed no clear visiting pattern (Figure 2). According to the chi-square test ( $\chi^2_8 = 4203$ ,  $p > 0.005$ ), the percentage of illegitimate visits (85%) was significantly greater than that of legitimate ones (15%). As far as standardized residuals are concerned, they proved that such differences are determined mainly by the visiting frequency of *H. mavors*, *M. tyrianthina*, *C. eos*, *E. ensifera* and *D. gloriosa*.

### Nectar production pattern: volume and concentration

The measured flowers showed different production patterns, with asynchronous peaks. However, upon averaging the daily values, some regularity was found. On the first day, nectar production took place only toward the end of the afternoon and volumes were very low (average of 5.1 $\mu$ l; SD= 0.83; n= 14). On the second day, the average was 182 $\mu$ l (SD= 8.24; n= 14), being the largest production compared with all other days, and production was erratic (Figure 3). On the third day, nectar volume decreased (average= 39.66 $\mu$ l; SD= 6.7; n= 14), a peak being observed only in the morning. Nectar volume varied significantly on the three days of anthesis ( $F_{1,13} = 18.8$ ;  $p < 0.0001$ ), but not among the flowers ( $F_{1,13} = 1.72$ ,  $P = 0.05$ ).

On the first day of anthesis, concentration tended to increase slightly in the late afternoon. On the second day, lower values were recorded early in the morning and at the end of the afternoon, while the pattern on the third day was very similar to that of the second day, except

that during the early morning hours, values were not quite as high (Figure 3). On the third day, nectar volume decreased (average =  $39.7 \pm 6.7 \mu\text{l}$ ), a peak being observed only in the morning. Nectar concentration averaged  $23.03 \pm 2.66\%$  and showed no significant differences among the days ( $F_{1,13} = 0.22$ ;  $P = 0.64$ ), but it did among flowers, fluctuating between 2 and 36.5% ( $F_{1,13} = 17.58$ ;  $p < 0.0001$ ). These flowers open at night.

The mean volume produced by day and the average of the second and third days showed no significant correlation with bird activity patterns, except for four cases in which a very low correlation was found: the first on day one with *C. eos* ( $r = 0.65$ ) and three on day two that involved *M. tyrianthina* ( $r = 0.64$ ), *D. gloriosa* ( $r = 0.67$ ) and *I. chrysater* ( $r = 0.62$ ).

### Reproductive biology

In the autogamy treatments and their control, 100% of the flowers aborted, while in the xenogamy treatment, 78.8% did so; that is, two out of nine flowers taken into consideration produced fruits. Seed production was 137 and 139 seeds per fruit in the two treatments. The stigmatic receptivity tests ( $n = 45$ ) were positive in 100% of cases.

### Effect of nectar robbing on the reproductive activity of the plant

Of the flowers marked during the low florescence interval (September-December 2005) that had suffered nectar robbing, 100% aborted, while 96.9% of the protected flowers did the same, which represents that one of the 31 observed flowers fructified and produced 117 seeds. In the experiments carried out during the florescence peak (March-September 2006), 38% of the robbed flowers and 96% of the unrobbed ones aborted. These results are contrary to expectation. Average seed production was  $151 \pm 7$  and  $81 \pm 16$ , respectively.

In view of the high percentage of abortions among the flowers used in September 2005, 21 fruits were randomly collected from the patches employed,

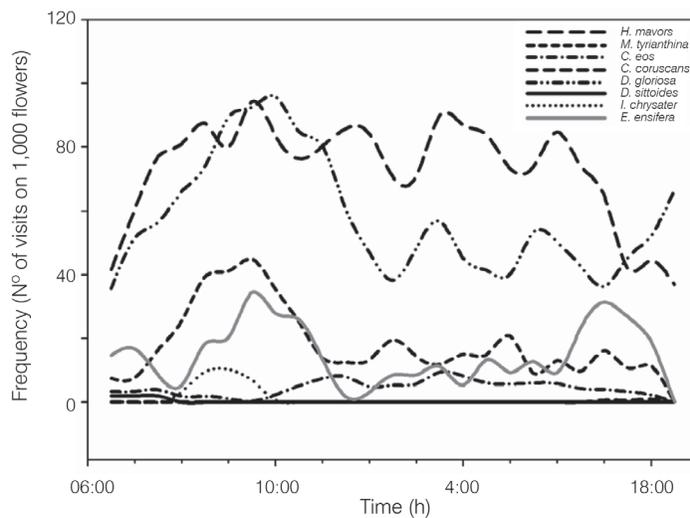


Figure 2. Frequency of visits throughout the day by bird species associated with *Passiflora mixta*.

in order to evaluate whether they showed evidence of having suffered nectar robbing, and calculated the average of the seeds produced per fruit. Although 100% of the fruits showed evidence of having suffered

nectar robbing, they produced an average of  $149 \pm 68.7$  seeds per fruit.

### Damage to the floral structures during the nectar robbing process

No visible differences in the reproductive structures of robbed and unrobbed flowers were detected. Hence, the nectar robbers apparently limited themselves to piercing holes only in the wall of the hypanthium, without harming anthers, stigmas, ovaries or androgynophore. Two types of scars were identified: one of them made by flower piercers (76%), which consisted of two holes, one circular and one elongated, corresponding to the penetration of the hypanthium by the lower and upper part of the bill, respectively; the other corresponds to bumblebees (24%), with holes and sizes of various shapes, since these animals chew the surface of the nectary. Scars of both types were located on the part of the hypanthium covering the nectary at an average of 6.6mm (SD = 0.26;  $n = 28$ ) from the base of the hypanthium. Inspection of the flowers showed that 77% of them had suffered nectar robbing.

### Discussion

In spite of the bird assemblage being located on the lower limit predicted by the Chao 2 richness estimator, the value obtained is a good approximation of reality, since the cause of the large confidence intervals in the estimator was the presence of *I. chrysater* and *C. coruscans*, species that are infrequent at the site; *I. chrysater* is found on the upper limit of its altitudinal distribution, while *C. coruscans* migrates between the cloud forest and páramo ecological units (Hilty, 2003; Rengifo *et al.*, 2005). In addition, these two species could be classified as occasional visitors since their frequency is considerably lower than other bird species. As far as *I. chrysater* is concerned, this is the first record of an Icteridae as a nectar robber, notwithstanding that the greater interrelation of this species with the plant must

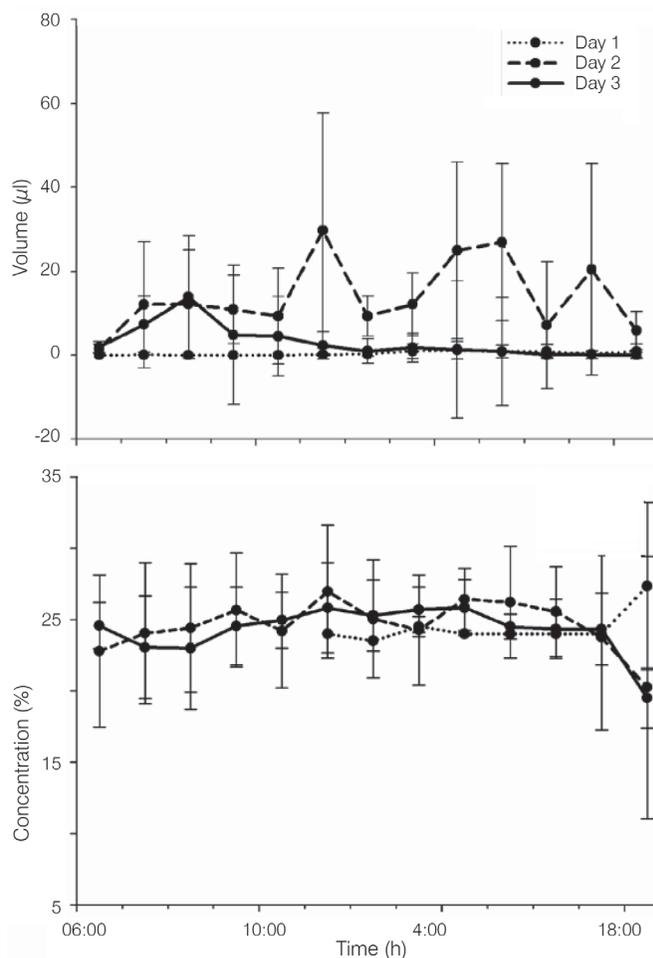


Figure 3. Sugar volume and concentration of nectar produced by *Passiflora mixta* flowers ( $n = 14$ ) during anthesis days. The bars represent the standard deviation for each point on the graphs.

be with its fruits. For this reason, together with *T. fuscater*, it should be considered as a potential seed disperser. *E. ensifera* is the only species exhibiting morphological correspondence with *P. mixta* flowers, which allows it to make legitimate visits (Table I). In spite of this, the nectar offered by these flowers was consumed by a significant number of nectarivorous species that, not having the anatomical attributes that allow them to visit the flowers frontally, make illegitimate visits, acting as nectar robbers. Additionally, the extraordinary length of the androgynophore ( $9.7 \pm 4.45\text{mm}$ ) does not allow an accidental contact of any part of the bodies of these animals with anthers or with stigmas, thereby preventing them from acting as accidental pollinators.

The foraging patterns of nectar robbers confirm the importance of this resource in their diet, since all of them showed high visit frequency throughout the day. Moreover, activities of *M. tyrinthina*, *C. eos* and *D. gloriosa* were positively correlated with the nectar production pattern. In spite of the lack of correlation between *E. ensifera* activity and nectar production, it shows two well defined peaks during the times of day when the energy demand is greater, that is, at the beginning of the morning and at the end of the afternoon (Gass and Garrison, 1999). This supports the importance of *P. mixta* in the energy budget of *E. ensifera*. The data obtained also shows that flower piercers are the most important robbers of these flowers, both because of the high visiting frequency and because they are mainly the ones that perforate and expose them to other avian visitors. All the holes made by the nectar robbers are found only on the surface that is occupied internally by the nectary.

The nectar production pattern of *P. mixta* is very similar to that of other high mountain species with anthesis lasting more than 1 day, with the larger volumes produced about mid-anthesis, and constant sugar concentration during all the days (Navarro, 2001). However, the present values of nectar volume and sugar concentration are greater than those reported for other ornithophilous flowers, both from high mountain and low land (Waser, 1979; Willmer and Corbet, 1981; Roubik *et al.*, 1985; Colwell, 1995; Arizmendi *et al.*, 1996; Lange *et al.*, 2000; Navarro, 2001).

Finding an erratic nectar production pattern on a populational level implies that nectar is available for the birds throughout the day, which explains that the most frequent nectar robbers show high visiting rates all day long. The fact that nectar production per flower is rela-

tively intermittent throughout the day and that these flowers are also robbed could be interpreted as a special case of bonanza-blank pattern (Feinsinger, 1978, 1983). Additionally, our data support the existence of self-incompatibility in *P. mixta* since, in spite of its low values, the xenogamy treatment was the only one where pollination was successful, which proves the importance of cross-fertilization in the reproductive success of the plants. Likewise, we interpret the abortion of all the flowers in the control treatment as another indication of self-incompatibility since it was evident that during the experiment, that took place out of the flowering peak, *E. ensifera* did not show the expected visit frequency.

The finding that 100% of the fruits collected in the field showed evidence of having been robbed suggests that the effect cannot be negative. On the contrary, evidence indicates a possible positive effect: 1) during the peak flowering period a greater number of aborted flowers was found among the unrobbed than the robbed ones, and 2) the robbed flowers produced a greater average number of seeds than unrobbed flowers. A possible explanation for this phenomenon is that if the nectar robbers diminish the resource available for the pollinator that must visit more flowers per time unit (Zimmerman and Cook, 1985), consequently incrementing pollen flow in the population, could be an adaptive advantage for this self-incompatible plant. Several studies have shown that higher floral visit frequency and longer visits lead to increased fruit and seed set (Thomson and Plowright, 1980; Feinsinger, 1983; Lanza *et al.*, 1995; Husband and Schemske, 1996). Moreover, since the pollinator is a trapliner species with high energy demands that must be satisfied by a mutualistic species that, like *P. mixta*, offers considerable nectar volume and concentration, the absence of robbers would allow the requirements of *E. ensifera* to be satisfied with fewer visits, thus reducing pollen flow and with it the probability of cross-pollination success.

In summary, in this study the reproductive success of *P. mixta* was determined mainly by the presence of its pollinator (*E. ensifera*) during the flowering peak months. Simultaneously, this success was favored by the visits of nectar robbers, which diminished the resource offered per flower and could be inducing an increase in pollen flow. Therefore, nectar robbers could be considered as an indirect mutualistic species of *P. mixta*.

#### ACKNOWLEDGEMENTS

The authors thank Teresa Schwarzkopf and Ilba López for logistical

support and assistance during field work, Jesús Lobo and Rafael Colmenares for allowing to carry out experiments on their land, and Pedro Jiménez, Javier Estrada, Daniel Larrea, Adriana Ruiz and Richard Smith for their valuable comments. Miguel Molinari made the taxonomic identification of the plants. The work was financed partially by CDCHT-ULA (Project C-1339-05-01-F) and IDEA WILD.

#### REFERENCES

- Addicott JF, Tyre AJ (1995) Cheating in an obligate mutualism: how often do yucca moths benefit yuccas? *Oikos* 72: 382-394.
- Arizmendi MC, Domínguez CA, Dirzo R (1996) The role of avian nectar robber and of hummingbird pollinators in the reproduction of two plant species. *Funct. Ecol.* 10: 119-127.
- Ataroff M, Sarmiento L (2003) *Diversidad en Los Andes de Venezuela. I. Mapa de Unidades Ecológicas del Estado Mérida*. Ediciones Instituto de Ciencias Ambientales y Ecológicas (ICAE), Universidad de Los Andes, Mérida, Venezuela. CD-ROM.
- Colwell RK (1995) Effects of nectar consumption by the hummingbird flower mite *Proctolaelaps kirmsei* on nectar availability in *Hamelia patens*. *Biotropica* 27: 206-217.
- Colwell RK (2005) *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*. Version 7.5. Persistent URL.
- Cotton PA (2001) The behavior and interactions of birds visiting *Erythrina fusca* flowers in the Colombian Amazon. *Biotropica* 33: 662-669.
- Escobar LK (1988) *Passifloraceae monografía 10*. Flora de Colombia. Instituto de Ciencias Naturales, Museo de Ciencia Natural, Universidad Nacional de Colombia. Bogotá. Colombia.
- Feinsinger P (1978) Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol. Monogr.* 48: 269-287.
- Feinsinger P (1983) Variable nectar secretion in a *Heliconia* species pollinated by hermit hummingbirds. *Biotropica* 15: 48-52.
- Garrison SE, Gass CL (1999) Response of a traplining hummingbird to changes in nectar availability. *Behav. Ecol.* 10: 714-725.
- Gass CL, Garrison SE (1999) Energy regulation by traplining hummingbirds. *Funct. Ecol.* 13: 483-492.
- Graves GR (1982) Pollination of a *Tristerix mistletoe* (Loranthaceae) by *Diglossa* (Ave, Thraupidae). *Biotropica* 14: 316-317.
- Gutiérrez-Z A, Carrillo E, Rojas S (2004a) *Guía Ilustrada de los Colibríes de la Reserva Natural Río Nambí*. FPA, FELCA, ECOTONO. Bogotá, Colombia. 156 pp.
- Gutiérrez-Z A, Rojas-Nossa S, Stiles G (2004b) Dinámica poblacional de la interacción colibrí-flor en ecosistemas altoandinos. *Ornitol. Neotrop.* 15: 205-213.
- Hilty SL (2003) *Birds of Venezuela*. 2<sup>nd</sup> ed. Princeton University Press. Princeton, NJ, USA. 876 pp.
- Husband BC, Schemske DW (1996) Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* 50: 54-70.
- Inouye DW (1980) The terminology of floral larceny. *Ecology* 61: 1251-1252.

- Irwin RE (2000) Hummingbird avoidance of nectar-robbled plants: spatial location or visual cues. *Oikos* 91: 499-506.
- Irwin RE, Brody AK (1998) Nectar robbing in *Ipomopsis aggregata*: effects on pollinator behavior and plant fitness. *Oecologia* 116: 519-527.
- Irwin RE, Brody AK, Waser NM (2001) The impact of floral larceny on individuals, populations and communities. *Oecologia* 129:161-168.
- Isler ML, Isler PR (1999) *Tanagers: Natural History, Distribution and Identification*. Smithsonian Institution Press. Washington, DC, USA. 406 pp.
- Kearns CA, Inouye DW (1993) *Techniques for Pollination Biologists*. University Press of Colorado. Niwot, CO, USA. 583 pp.
- Kjonaas C, Rengifo C (2006) Differential effects of avian nectar robbing on fruit set of two Venezuelan Andean cloud forest plants. *Biotropica* 38: 1-4.
- Lara C, Ornelas JF (2001) Preferential nectar robbing of flowers with long corollas: experimental studies of two hummingbird species visiting three plant species. *Oecologia* 128: 263-273.
- Lange RS, Scobell SA, Scott PE (2000) Hummingbird-syndrome traits, breeding system and pollination effectiveness in two syntopic *Penstemon* species. *Int. J. Plant Sci.* 161: 253-263.
- Lanza Z, Smith GC, Sack S, Cash A (1995) Variation in nectar volume and composition of *Impatiens capensis* at the individual, plant, and population levels. *Oecologia* 102: 113-119.
- Lindberg AB, Olesen JM (2001) The fragility of extreme specialization: *Passiflora mixta* and its pollinating hummingbird *Ensifera ensifera*. *J. Trop. Ecol.* 17: 323-329.
- Lyon DL, Chadek C (1971) Exploitation of nectar resources by hummingbirds, bees (*Bombus*) and *Diglossa baritula* and its role in the evolution of *Penstemon kunthii*. *Condor* 73: 246-248.
- Maloof JE, Inouye DW (2000) Are nectar robbers cheaters or mutualists? *Ecology* 81: 2651-2661.
- Morris WF (1996) Mutualism denied? Nectar-robbing bumblebees do not reduce female or male success of bluebells. *Ecology* 77: 1451-1462.
- Navarro L (2001) Reproductive biology and effect of nectar robbing on fruit production in *Macleania bullata* (Ericaceae). *Plant Ecol.* 152: 59-65.
- Rengifo C, Nava A, Zambrano M (2005) *Lista de Aves de La Mucuy y Mucubaji. Parque Nacional Sierra Nevada, Mérida-Venezuela. Serie Aves de Mérida. Vol. 1. Editorial Venezolana. Mérida, Venezuela.*
- Roubik DW, Holdbrook NM, Parra G (1985) Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia* 66: 161-167.
- Snow DW, Snow BK (1980) Relationship between hummingbirds and flowers in the Andes of Colombia. *Bull. Br. Mus. Nat. Hist. (Zool.)* 38: 105-139.
- Thomson JD, Plowright RC (1980) Pollen carryover, nectar rewards, and pollinator behavior with special reference to *Diervilla conicera*. *Oecologia* 46: 68-74.
- Traveset A, Willson MF, Sabag C (1998) Effects of nectar-robbing birds on fruit set of *Fuchsia magellanica* in Tierra del Fuego: a disrupted mutualism. *Funct. Ecol.* 12: 459-464.
- Tyre AJ, Addicott JF (1993) Facultative non-mutualistic behaviour by an "obligate" mutualist: "cheating" by yucca moths. *Oecologia* 94: 173-175.
- Waser NM (1979) Pollinator availability as a determinant of flowering time in ocotilo (*Fouquieria splendens*). *Oecologia* 39: 107-121.
- Willmer PG, Corbet SA (1981) Temporal and microclimatic partitioning of the floral resources of *Justicia aurea* amongst a concourse of pollen vectors and nectar robbers. *Oecologia* 51: 67-78.
- Zar JH (1999) *Biostatistical Analysis*. 4th ed. Prentice Hall. Upper Saddle River, NJ, USA. 663 pp.
- Zimmerman M, Cook S (1985) Pollinator foraging, experimental nectar-robbing and plant fitness in *Impatiens capensis*. *Am. Midland Nat.* 143: 84-90.

## AVES LADRONAS DE NÉCTAR DE *Passiflora mixta* (Passifloraceae) ¿TIENEN EFECTO POSITIVO EN LA PLANTA?

Roxibell C. Pelayo, Carlos Rengifo y Pascual J. Soriano

### RESUMEN

El efecto del robo de néctar sobre la reproducción de plantas puede ser negativo, positivo o neutro. Se evaluó su efecto en *Passiflora mixta*, una planta de la alta montaña andina que es polinizada por el colibrí pico de espada (*Ensifera ensifera*). Se determinó (1) el ensamble de aves asociados a las flores de *P. mixta*, (2) el patrón de producción de néctar de las flores de *P. mixta*, (3) cómo el robo de néctar afecta la producción de frutos y semillas, y (4) la auto-incompatibilidad en las flores de esta especie. Encontramos que ocho especies de aves se asocian con las flores

de *P. mixta*: cinco colibríes, dos diglosas y un icterido. Los experimentos apoyan la auto-incompatibilidad de la planta. Los ladrones de néctar no dañan las estructuras reproductivas de las flores. Se concluye que en este sistema el efecto del robo de néctar podría ser positivo; pues los ladrones al disminuir el néctar ofrecido por las flores, inducirían un aumento en el flujo de polen. En consecuencia, la establecida entre *P. mixta* y sus ladrones de néctar puede ser considerada como una relación indirecta mutualista.

## AVES LADRAS DE NÉCTAR DE *Passiflora mixta* (Passifloraceae) TÊM EFEITO POSITIVO NA PLANTA?

Roxibell C. Pelayo, Carlos Rengifo e Pascual J. Soriano

### RESUMO

O efeito do roubo de néctar na reprodução das plantas pode ser negativo, positivo ou neutro. Tal efeito foi avaliado em *Passiflora mixta*, espécie de altas montanhas andinas que é polinizada pelo beija-flor-bico-de-espada (*Ensifera ensifera*). Determinaram-se: 1) o conjunto de pássaros associados às flores de *P. mixta*, 2) o padrão de produção do néctar de *P. mixta*, 3) a maneira em que o roubo de néctar afeta a produção de frutos e sementes, e 4) a autoincompatibilidade nesta espécie. Encontraram-se oito espécies de pássaros associadas a flores

de *P. mixta*: cinco beija-flores, dois picaflores e um corruipião. Os experimentos apoiam a autoincompatibilidade da planta. Os ladrões de néctar não danificam a estrutura reprodutiva da planta. O efeito do roubo de néctar parece ser positivo, já que os ladrões diminuem o recurso oferecido, incrementando o fluxo de pólen. Em consequência, o efeito dos ladrões de néctar em *P. mixta* poderia ser considerado como uma relação de mutualismo indireto.