Multiple ecological interactions: nectar robbers and hummingbirds in a highland forest in Mexico

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Abstract: Nectar robbers are animals that extract the nectar produced by plants without effecting pollination. These animals can have negative, positive, or neutral effects on the interaction, depending on the direct and indirect effects of each participant in the system. The purpose of this work was to analyze the prevalence of nectar robbing and its temporal dynamics in a tropical highland forest in western Mexico. The system was studied in terms of the seasonal changes in (*i*) specific composition and abundance of hummingbird pollinators, their hosts, and the nectar robbers, (*ii*) use of resources by the nectarivorous birds and flowers, and (*iii*) prevalence of flower piercing by the cinnamon flowerpiercer, *Diglossa baritula*. The guild consisted of 17 species of hummingbirds, 2 species of nectar robbers, and 21 plant species that were visited by nectarivorous birds (robbers and pollinators). The relative abundance of birds and available flowers showed two peaks, one in winter and the other in the rainy season. Some plant species were used more than expected from their abundance. Overlap in the use of flowers among hummingbirds and also between hummingbirds and the nectar robbers was high. Nectar robbing was found to be widespread, occurring in almost all of the plants known to be hummingbird pollinated. The ratio of hummingbirds to nectar robbers was around 10 throughout the year.

Résumé : Les voleurs de nectar sont des animaux qui extraient le nectar des plantes sans participer à leur pollinisation. Ces animaux peuvent avoir des effets négatifs, positifs ou neutres sur les interactions du système selon les effets directs et indirects de chaque participant. Le but de cette étude est d'analyser la fréquence des vols de nectar et leur dynamique temporelle dans une forêt tropicale des terres hautes de l'ouest du Mexique. Les changements saisonniers du système ont été étudiés sous plusieurs aspects : (*i*) la composition en espèces et l'abondance des colibris pollinisateurs, de leurs hôtes et des voleurs de nectar, (*ii*) l'utilisation des ressources par les oiseaux nectarivores et les fleurs et (*iii*) la fréquence du perçage des fleurs par *Diglossa baritula*. La guilde est composée de 17 espèces de colibris, 2 voleurs de nectar et 21 espèces de plantes visitées par les oiseaux nectarivores (voleurs de nectar et pollinisateurs). Deux pics ont été observés dans l'abondance relative des oiseaux et la disponibilité des fleurs, l'un en hiver et l'autre au cours de la saison des pluies. Certaines plantes ont été utilisées plus souvent que prévu d'après leur abondance. Il y a un important chevauchement dans l'utilisation des fleurs parmi les colibris et entre les colibris et les voleurs de nectar. Le vol de nectar s'est avéré une tactique répandue, chez presque toutes les plantes que l'on sait pollinisées par les colibris. Le rapport nombre de colibris/nombre de voleurs de nectar est d'environ 10 pendant presque toute l'année.

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Introduction

Floral visitors that obtain nectar by piercing floral tissues without contacting the anthers and the stigma are called nectar robbers (Inouye 1983). Nectar robbers can reduce plant fitness by depleting nectar (Navarro 1999, 2001), damaging reproductive parts (McDade and Kinsman 1980), and driving pollinators away (Roubick 1982). They can compete directly either by excluding pollinators from flowers or by depleting nectar (Roubick 1982; Navarro 1999, 2001). On the other hand, by depleting flowers of nectar, robbers may force pollinators to visit more flowers, thereby potentially increasing outcrossing distance rate, which may be advantageous for the plant (Fritz and Morse 1981; Gill et al. 1982; Inouye

1983). Nectar robbers can sometimes promote pollination, if movements during piercing lead to the transference of gametes between reproductive parts inside a flower (Hawkins 1961; Higashy et al. 1998; Navarro 2001) or when the robber is accidentally dusted with pollen that is then transported to the next flower (Macior 1966; Koeman-Kwak 1973; Graves 1982). They can also be commensals of both plants and pollinators if (*i*) nectar is not a limiting factor for pollinators and nectar availability is not affected by the piercing, (*ii*) no damage is done to the reproductive parts of the flower, and (*iii*) the cost of nectar production for the plant is low (Arizmendi et al. 1996).

Among bird-pollinated plants, the occurrence of nectar robbery is common (McDade and Kinsman 1980; Wilmer and Corbet 1981; Carpenter et al. 1993; Powers and Conley 1994; Arizmendi et al. 1996; Bittrich and Amaral 1996; Traveset et al. 1998; Irwin and Brody 1998, 1999; Navarro 2001). However, the relative importance of nectar robbers for a community of bird pollinators and their food plants has received little attention and forms the focus of this study.

The effect of nectar robbers upon a pollination system depends not only on their direct effect on individual flowers

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but also on the abundance and relative frequency of pollinators, robbers, and plants (flowers) and on the way these fluctuate through time (Soberón and Martínez del Río 1985). If pollinators greatly outnumber robbers, then the probability that a flower will be pollinated before it is robbed is high, and hence, robbery might not be expected to have negative effects on the reproductive success of plants under these circumstances. Thus, to fully evaluate the effect of the robber on a pollination system, it is necessary to assess the temporal and spatial variation in species composition and abundance of the three components (flowers, pollinators, and robbers).

The tropical montane forests of western Mexico have complex communities of hummingbirds (21 species throughout the year), food plants (more than 20 species), and avian nectar robbers (mainly the cinnamon flowerpiercer, *Diglossa baritula*) (Ornelas and Arizmendi 1995). They represent an ideal system for the study of multiple-species interactions. The purpose of this work is to provide a general description of the temporal dynamics of flower availability and use by hummingbird pollinators and nectar robbers. Specifically, I describe variation, within a single year, in the availability of flowers of hummingbird-pollinated plants, pollinators, and nectar robbers as well as the prevalence and incidence of nectar robbery in terms of resources used.

Materials and methods

Study area
Variation in the abundance of hummingbirds, hummingbird-pollinated flowers per plant species, and nectar robbers was assessed during monthly visits (8–10 days) to the Laboratorio Natural Las Joyas in the Sierra de Manantlán from November 1990 to October 1991. This reserve is located between the Mexican states of Jalisco and Colima, about 50 km east of the Pacific coast in western Mexico (19°35′N, 104°16′W). The Laboratorio Natural Las Joyas, a 1245-ha preserve owned by the Universidad de Guadalajara, is situated at 1952 m above sea level. Mean annual precipitation is 1609 mm (mean of 5 years), with most of the rain falling between June and October.

The mean annual temperature is 14.6°C, with very few days with temperatures below the freezing point. The vegetation is a mosaic of humid coniferous forest, pine–oak forest, patches of cloud forest located in ravines, and secondary vegetation from burning of the original forest or in abandoned agricultural areas. A detailed analysis of the structure and composition of the vegetation is given in Guzmán (1985), Saldaña-Acosta and Jardel (1991), and Vázquez et al. (1990).

Flower availability
Plants in bloom were monitored to determine which species were visited by robbers and (or) hummingbirds and how visitation rates varied throughout the year. Observations were carried out during the first and second days (early morning, half an hour after sunrise) of each monthly visit. An observer stood in front of an individual plant or patch of each of the blooming plant species and monitored an area, never exceeding 3.5 m in diameter, of each blooming plant species. A plant was recorded as visited by a nectar robber only when the bird was observed piercing a flower. In the case of hummingbird pollinators, a visit was defined as an instance in which a bird probed at least one flower. Observations were carried out in the early morning (beginning half an hour after sunrise) and lasted up to 2 h. If no visits occurred within 2 h, the observation period was ended. In all cases, the visiting species was re-

corded. All of the species in bloom each month were included in the surveys.

To complement the observations of bird visits during the monthly censuses of flower availability (see below), holes made in flowers by nectar robbers were noted for each plant species. The frequency of occurrence was determined by calculating the percentage of damaged flowers per individual plant and the percentage of individual plants that had some level of damage. *Diglossa baritula* steals nectar by making a small hole in the base of the corolla, using its upper mandible as a hook to hold the flower still while it pierces the corolla with its lower mandible (Skutch 1954; Colwell 1973).

Temporal changes in the availability of flowers visited by hummingbirds were assessed by monthly censuses of flowers in four permanent transects of 3000 m^2 (300 m long × 10 m wide). The transects were located within areas with two contrasting vegetation types, chosen as representative of the study area (i.e., representing the composition of about 90% of the zone; Saldaña-Acosta and Jardel 1991): forested and regrowth after fire. Two transects were located within each vegetation type by randomly selecting a numeral that represented the number of metres from the beginning of a trail where transects were to be located. Two transects were established in the forested area, which comprises humid pine forest and pine forest – cloud forest transition, while the other two were located in a patch of burned regrowth (burned about 15 years ago; hereafter referred to as the nonforested area). For each blooming species either directly observed or suspected from its floral syndrome (as defined by Faegri and van der Pijl 1979) as being visited by hummingbirds, the number of flowers visited per individual (or per patch in cases where it was impossible to distinguish individuals), the number of inflorescences, and the number of flowers per inflorescence, when appropriate, were recorded. Plant specimens were collected for further identification at the National Herbarium of Mexico. To test for differences in flower abundance between and within the two monthly-censused areas, a generalized linear model (GLM ANOVA for repeated measures) was performed using PROC GLM in SAS (SAS Institute Inc. 1985) with the log-transformed data (log x + 1), using transects within an area as replicates.

Nectar production was measured in plants where abundant flowers were present throughout the year. Flower buds were closed with mosquito-net bags before opening, and nectar production by 30 individual flowers for each plant species analyzed was measured over 24 h. The amount of nectar produced (in microlitres) was measured using calibrated micropipettes, and sugar concentration was measured using a hand-held refractometer. The number of calories produced per flower was calculated using the formula in Scogin (1985).

Bird sampling
Monthly variation in the abundance of nectarivorous birds was assessed by placing eight mist nets (12 × 3 m) for 8 h (beginning at dawn) over 2 consecutive days in each of the two vegetation areas used for flower-availability censuses (forested and nonforested areas). Nets were placed 100 m apart on each transect, beginning at the same point as the vegetation transects.

Each bird caught was marked with a numbered individual band. Relative abundance per species (number of individuals caught per 576 m^2, i.e., 3 × 12 m nets × 8 nets × 2 days) was calculated per month per transect, disregarding all repeated captures of the same individuals.

Flower use by hummingbirds
Bird visitation to specific plant species was assessed by making permanent pollen preparations with pollen loads from each bird caught (from forehead, breast, and bill) in the nets used for

monthly sampling of birds (described above). Pollen obtained from birds was compared with a reference pollen collection developed from pollen samples obtained directly from all species detected in the flower-availability censuses. Permanent pollen preparations were produced using a fuchsin-stained gel following Beattie (1971).

The number of individuals of each hummingbird species on which the pollen of a particular species appeared was used to describe patterns of plant use by hummingbirds for each month sampled. Differential use was evaluated by comparing observed numbers of hummingbirds that bore pollen from the different plant species with expected numbers calculated according to two hypotheses: the first one concerned the relative abundance of flowers as a measure of resource availability, and the second one related to mean calories produced by each plant species. Chi-squared tests were performed for the six hummingbird species most often captured ($N > 30$ individuals captured). The significance level taken was 0.0041 (Bonferroni corrections for repeated tests 0.05/12). For caloric contents, we used only plant species (see above) for which we have data.

Prevalence and incidence of nectar robbery

Visitation by the robbers was assessed by the direct and indirect methods described above. To test for effects of flower piercing on female fitness under nonmanipulative conditions, I observed seed production by damaged and undamaged flowers of the two more abundant flower species visited by *D. baritula* and *Vermivora ruficapilla*.

In 30 randomly chosen individuals of *Salvia mexicana* and 28 of *Salvia iodantha*, I marked 1 pierced and 1 nonpierced flower (2 flowers in 30–28 different plants). Flowers were chosen randomly and followed until seed set. I then counted seeds from both groups of flowers. Flowers of both plant species lasted 4 days. Calyces were marked on the afternoon of the last day. After marking, corollas were separated from calyces to ensure no further visitation. Differences in seed production between pierced and nonpierced flowers were assessed with a paired-sample t test.

For the other nectar robber, *V. ruficapilla*, 30 randomly chosen flowers of *S. mexicana* and 30 of *S. iodantha* were marked after being robbed and were followed until seed production.

Results

Annual variation in flower production

Of all the plant species that bloomed during the year of study, 21 were visited by hummingbirds. The list of visited species and an estimation of their production of flowers are shown in Fig. 1. The number of hummingbird-visited species per month ranged from 3 (July) to 12 (September). Flower production varied considerably throughout the year, and there were two distinct blooming peaks. The first occurred during the dry season, from December through February, with a total of 2 751 – 21 980 flowers per month and 9 or 10 species in bloom. The second peak occurred in the late wet season, in September, with 20 665 flowers and 12 species in bloom (Fig. 1).

The numbers of flowers per transect were statistically indistinguishable within the two censused areas (transects within an area were not distinguishable: repeated-measures GLM ANOVA, $F_{[1,2]} = 1.2$, $P > 0.38$), so data from transects were clumped for each area for further analysis. There was considerable variation in the number of flowers between areas throughout the year (Fig. 2A). In the dry season (December–February) the nonforested area showed a marked increase in the number of flowers, due almost completely to

Fig. 1. Abundance of flowers produced by different plant species throughout the year (November to October) in Manantlán, Jalisco, México, according to their flowering period. Astericks are the number of flowers × 10.
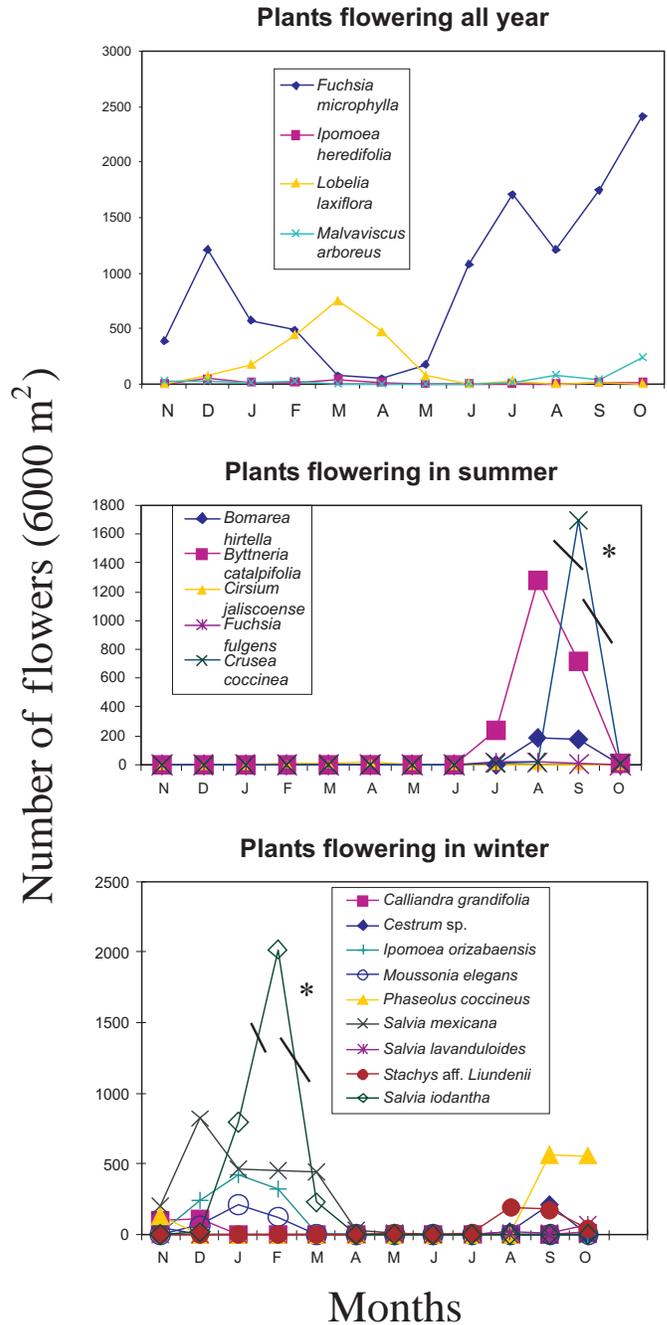
the blooming of *S. iodantha* (cf. Fig. 1). During the second flowering peak, in September, the number of flowers in all transects increased, but the increment in the forested area was higher (Fig. 2A), with *Crusea coccinea* contributing 51% of the total number of flowers produced in the nonforested area and 93.8% in the forested area.

Table 1. Plant life form and morphological features of flowers visited by hummingbirds and nectar robbers in Manantlán, Jalisco.

Plant species	Biological form	Flower shape	Color	Arrangement	Pollinator[a]
Bomarea hirtella	Herb	Tube	Orange	Inflorescence	H
Byttneria catalpifolia	Shrub	Cup	Yellow	Solitary	I, H, PB
Calliandra grandifolia	Tree	Cup	Red	Inflorescence	H, PB
Castilleja sp.	Herb	Tube	Red	Solitary	H, I
Cestrum sp.	Shrub	Tube	Yellow	Inflorescence	H, I
Cirsium jaliscoense	Shrub	Cup	Cream	Inflorescence	H, PB
Crusea coccinea	Herb	Tube	Red	Inflorescence	H
Fuchsia microphylla	Shrub	Tube	Red	Solitary	H, I
Fuchsia fulgens	Vine	Tube	Red	Solitary	H
Ipomoea heredifolia	Vine	Tube	Orange	Solitary	H
Ipomoea orizabaensis	Vine	Tube	Purple	Solitary	H, I
Lobelia laxiflora	Shrub	Tube	Orange	Inflorescence	H
Malvaviscus arboreus	Shrub	Tube	Red	Solitary	H
Moussonia elegans	Shrub	Tube	Orange	Solitary	H, I
Phaseolus coccineus	Shrub	Tube	Red	Solitary	H, I
Psittacanthus ramiflorus	Hemiparasite	Tube	Orange	Inflorescence	H
Salvia lavanduloides	Herb	Tube	Purple	Solitary	I, H
Salvia mexicana	Shrub	Tube	Purple	Solitary	H
Salvia iodantha	Shrub	Tube	Red	Solitary	H
Stachys aff. *liundenii*	Herb	Tube	Pink	Solitary	H, I
Tillandsia sp.	Epiphyte	Tube	Orange	Inflorescence	H

[a]H, hummingbird; I, insect; PB, perching bird.

Eleven out of the 21 plant species (52.4%) visited by nectarivorous birds (Table 1) were herbs and 4 (19.05%) were shrubs. The rest were vines or epiphytes. Only 3 of the 21 species had cup-shaped flowers, the majority being tubular. The 21 species of visited plants bore flowers whose color was close to red, with a predominance of red (35%) and orange (30%) flowers.

Nectar production varied to a great extent among the nine species examined (Fig. 3). In terms of quantity of nectar, one group of species produced less than 5 μL per flower, on average (*Fuchsia microphylla*, *C. coccinea*, *S. iodantha*, and *Cirsium jaliscoense*). Another two species produced around 10 μL (*Calliandra grandifolia* and *S. mexicana*) and the last two species produced more than 15 μL of nectar per flower (*Lobelia laxiflora* and *Ipomoea heredifolia*). Sugar concentration varied less, being around 20% in most of the plants except *C. coccinea* in which it is around 10%. The number of calories produced per flower was high in *I. heredifolia* and *L. laxiflora* (more than 150 calories per flower), intermediate (around 100 calories) in *Malvabiscus arboreus*, *S. mexicana*, and *Calliandra grandifolia*, and low (less than 50 calories) in the rest of the studied species (Fig. 3).

Birds

Seventeen species of hummingbirds and 2 species of nectarivorous passerine birds were caught during the year of netting (Fig. 4). The number of species ranged from 5 to 14 per month, with February showing the largest number of species and individuals. The hummingbird community was composed of four resident species, seven winter visitors (five of which were latitudinal migrants and two were tropical wanderers, spending more than half of the year in the area and migrating altitudinally), and five summer visitors that

were also altitudinal migrants but stayed in the area for less than 3 months (Fig. 4). Two nectar robbers were detected: one resident (*D. baritula*) and one winter visitor (*V. ruficapilla*) that was caught only in February (Fig. 4). The winter visitors stayed in the area for periods ranging from 1 month, February (three species) or January (one species), to the whole winter season (three species). With the exception of *Phaethornis superciliosus*, which stayed in the area for about 3 months, the summer visitors remained only for 1 month. The altitudinal migrants stayed in the area from winter to early summer.

The abundance of nectarivorous birds changed considerably throughout the year. Numbers ranged (summing data for the two areas censused) from 13 individuals caught in October to 288 in February. Differences in abundance of birds between areas and months were assessed by a multiple contingency table analyzed by means of generalized linear models with a log link function (Baker and Nelder 1978; Healy 1988). Because the response variable consists of counts (number of birds caught per month per transect), error was declared as Poisson (Healy 1988). The difference in the relative abundance of hummingbirds between areas was significant (log-linear model, $\chi^2_3 = 86\,010$, $P < 0.005$). There were two marked peaks of abundance during the year in the non-forested transects (Fig. 2B). In the forested area, numbers were small throughout the year, showing an increase in the rainy season, from June to September. In the nonforested area, numbers remained comparatively high throughout the year, but there were abrupt increases in February and June. The first peak can be explained by the arrival of long-distance migrants and the second by the arrival of the altitudinal vagrants that visited the area for a short time.

Eight of 17 species of hummingbirds plus the robber

Fig. 2. Abundances of flower species visited by hummingbirds and nectarivorous birds (A) and the number of nectarivorous birds captured (B) in the forested area (■) and the nonforested area (+) censused in Manantlán throughout the year (November to October).
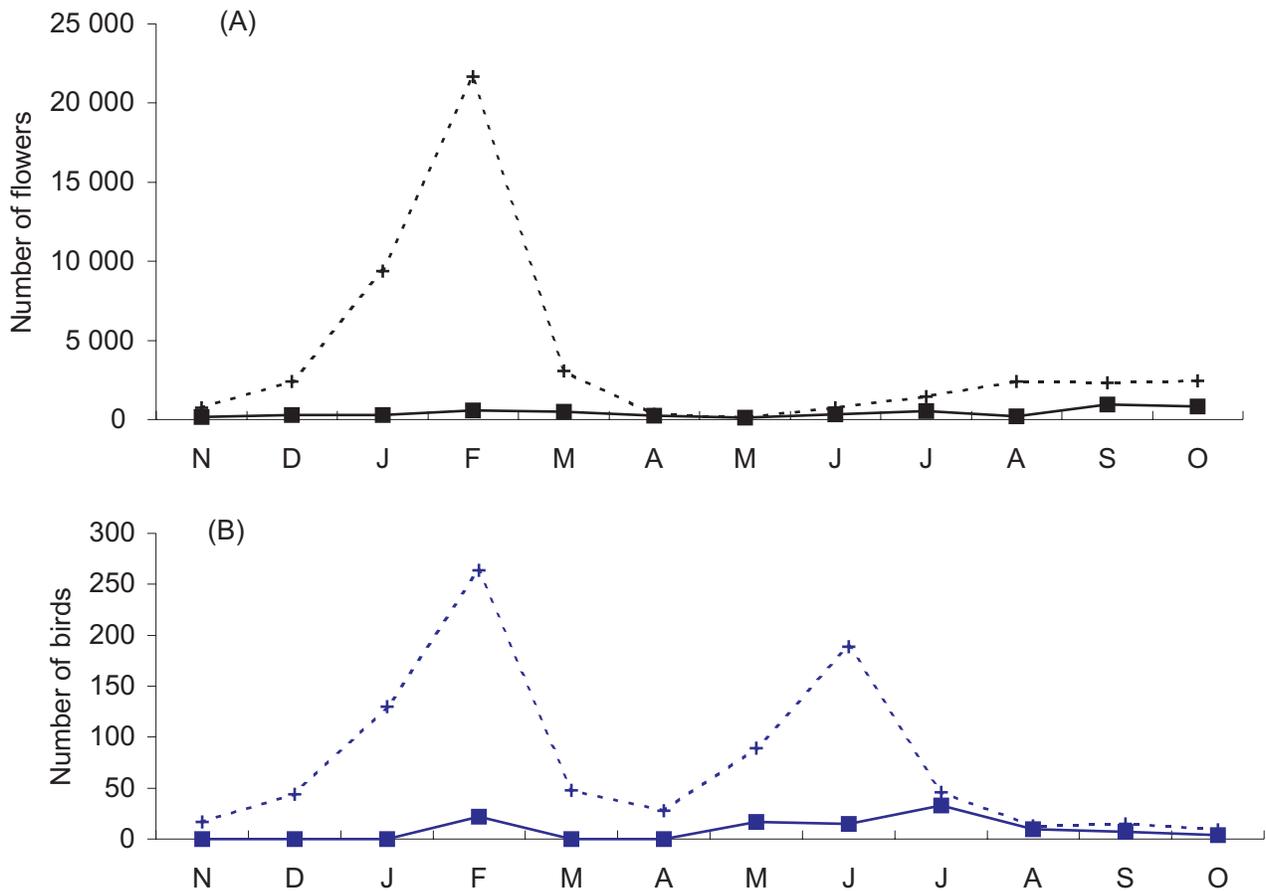
D. baritula were captured in both vegetation areas. The other nine species (*Archilochus alexandrii*, *Amazilia rutila*, *Amazilia violiceps*, *Calothorax lucifer*, *Cynanthus latirostris*, *Stellula calliope*, *Selasphorus rufus*, *Selasphorus sassin*, and *Tilmatura dupontii*) and the robber *V. ruficapilla* were only found in the nonforested area. Nine species were recorded in both areas, but in general, all nectarivorous bird species were considerably more abundant in the nonforested area. All species with the exception of *P. superciliosus* ($\chi^2_1 = 1.5$, df = 1, $P > 0.1$) and *Lampornis amethysthinus* ($\chi^2_1 = 7.06$, $P > 0.005$) were statistically more abundant in the nonforested area ($\chi^2_1 = 185.5$ for *A. beryllina*, 29.64 for *Atthis heloisa*, 32.59 for *Colibri thalassinus*, 28.48 for *D. baritula*, 12.04 for *Eugenes fulgens*, 173.91 for *Hylocharis leucotis*, and 12.97 for *Selasphorus platycercus*; $P < 0.005$ in all cases; Yates and Bonferroni corrections were used (Zar 1984)).

The ratio of hummingbird abundance to robber abundance showed that throughout the year, pollinators were more abundant than robbers (Fig. 5), with 5 (April) to 60 (June) times more pollinators than robbers.

**Patterns of interaction between plants and birds**

Some plant species were visited during almost all of their blooming period, or at least at their blooming peak, by many species of pollinators. *Hylocharis leucotis* and *L. amethysinus* were the most common visitors to all plants year-round. The least-visited plant species was the long-tubed *Fuchsia fulgens*

(*P. superciliosus* and *E. fulgens* and, with lower frequency, *A. rutila*). *Phaethornis superciliosus* was only recorded visiting *F. fulgens*, *Psittacanthus ramiflorus*, and *L. laxiflora*.

For all hummingbird species examined except one, both the explanation related to the relative abundance of flowers and that related to the calories produced by them were rejected, indicating that all hummingbird species preferred some plant species over others, regardless of their proportional abundance or the reward they produced (*A. beryllina*: abundance, $\chi^2 = 285.31$, df = 12, $P < 0.001$; calories, χ^2 142.83, df = 7, $P < 0.001$; *A. heloisa*: abundance, $\chi^2 = 22.48$, df = 11, $P < 0.001$; calories, $\chi^2 = 10.849$, df = 5, $P = 0.054$; *Colibri thalassinus*: $\chi^2 = 22.585$, df = 12, $P < 0.001$; calories, $\chi^2 = 21.52$, df = 6, $P = 0.001$; *H. leucotis*: abundance, $\chi^2 = 210.13$, df = 15, $P < 0.001$; calories, $\chi^2 = 146.51$, df = 7, $P < 0.001$; *L. amethystinus*: abundance, $\chi^2 = 160.16$, df = 15, $P < 0.001$; calories, $\chi^2 = 145.72$, df = 8, $P < 0.001$; *S. rufus*: abundance, $\chi^2 = 32.46$, df = 9, $P < 0.001$; calories, $\chi^2 = 25.68$, df = 5, $P < 0.001$). The only exception was *A. heloisa*, which visited flowers according to the caloric content of their reward.

In general, both *S. mexicana* and *S. iodantha* were visited more than expected from their abundance or their energetic content, while *C. coccinea* was visited less than expected. Hummingbird species that stayed for less time in the area tended to concentrate more on a few plant species in which many of them forage (Table 2), while residents used a wide

Fig. 3. Nectar production by nine common plant species in Manantlán. Data shown are the mean amount of nectar in microlitres produced per flower over 24 h ($N = 30$; open bars), the mean percentage of sugars present in nectar (solid bars), and the calories produced per flower over this time period (▲).
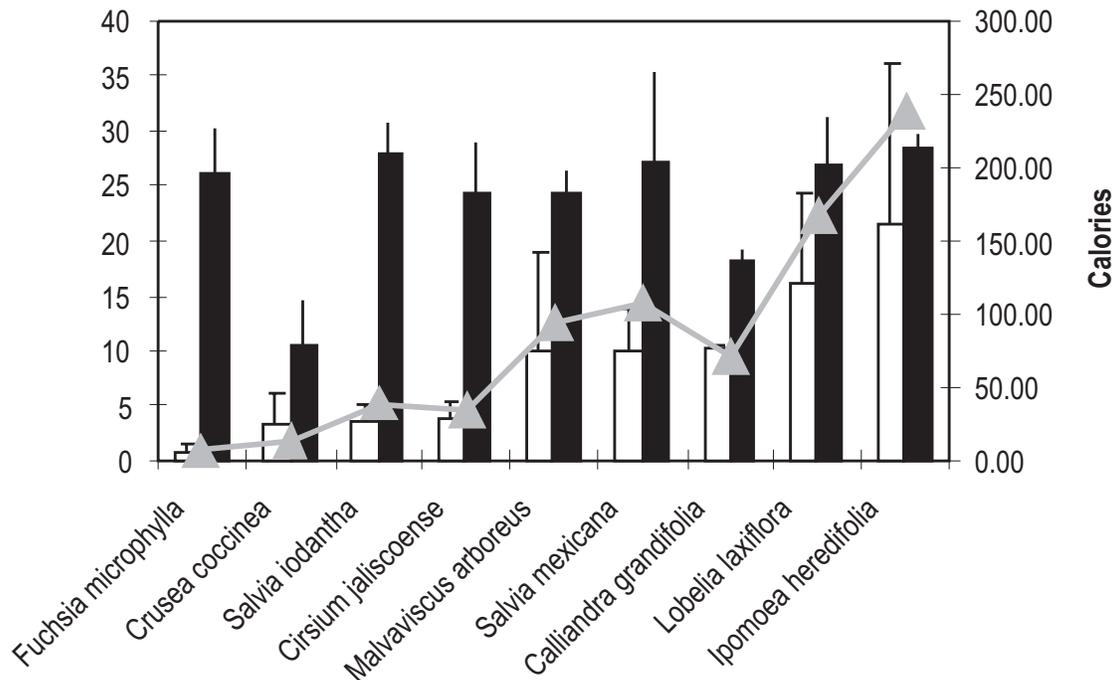
array of the available resources. Plants that produced more nectar with a higher sugar concentration, such as *L. laxiflora* (Fig. 3), were visited more than expected. However, *I. heredifolia*, which produced high-quality nectar, was generally visited less than expected. It is also important to note that there are morphological constraints that can drive flower selection. For example, *H. leucotis*, a short-billed species, concentrated to a great extent on short-tubed species such as *Bomarea hirtella* and *Salvia lavanduloides*.

Flower use by pollinators and robbers

An interaction matrix showing the proportion of hummingbirds of each species on which pollen of a given plant species was found is presented in Table 2. The proportion was calculated as the number of hummingbirds of each species that bore pollen divided by the total number of hummingbirds of each species captured. This measure represents proof of visitation and the frequency of pollen inside a hummingbird species a measure of the prevalence of flower use by the population sampled.

The interaction matrix shows that while pollen of some plant species (e.g., *M. arboreus*) was present on only a few hummingbirds of a few species, pollen of others (e.g., *S. mexicana* and *S. iodantha*) was present on many bird species and on many individuals within species. However, while some hummingbird species carried pollen from only a few plant species (e.g., *T. dupontii*), others (e.g., *L. amethysthinus*) bore pollen from almost all plant species. Individual pollen loads were, in general, mixed.

Diglossa baritula visited all hummingbird-visited flowers except *C. coccinea*, *Stachys* aff. *liundenii*, and *S. lavanduloides*, all of which are small herbs that cannot support the weight of *D. baritula*. For most of the year, *D. baritula* visited more

than 85% of the plant species pollinated by hummingbirds. Additionally, I found pollen of *P. ramiflorus*, *C. jaliscoense*, *Bytnneria catalpifolia*, and *C. grandifolia* on the head of *D. baritula*.

There was considerable variation in the percentage of damaged flowers per plant among the four species assessed. The mean percentages were 57.6% for *S. mexicana* ($N = 30$ individuals), 53.4% for *S. iodantha* ($N = 20$), 31.4% for *I. heredifolia* ($N = 10$), and 8.5% for *L. laxiflora* ($N = 10$).

The damage caused by *D. baritula* does not prevent seed production. No difference between the mean numbers of seeds produced by damaged and undamaged flowers could be detected (*S. mexicana*: mean number of damaged seeds = 1.82, mean number of undamaged seeds = 1.55, $t = 0.477$, df = 29, $P > 0.5$; *S. iodantha* mean number of damaged seeds = 1.72, mean number of undamaged seeds = 1.31, $t = 0.552$, df = 27, $P > 0.5$). However, a much larger sample size might reveal differences.

Vermivora ruficapilla was observed robbing *S. mexicana* and *S. iodantha* flowers in February, taking individual flowers from calyces, chewing nectar from the bottom of the corolla, and throwing away the corolla (along with the stamens). It was a very abundant migratory species (71 individuals were caught in 1 month) in the nonforested areas but was present in the area for only a short time. No seeds were produced by damaged flowers of the two plant species observed.

Diglossa baritula as a potential pollinator

Pollen grains of four plant species were found on the head of *D. baritula*. Two of them (*C. grandifolia* and *C. jaliscoense*) produce cup-shaped flowers that are visited by hummingbirds, perching birds, and insects. *Diglossa baritula* exploited these plants by using the "appropriate" entrance, without

Fig. 4. Abundances of nectarivorous bird species found throughout the year (November to October) in Manantlán, according to their migratory status.
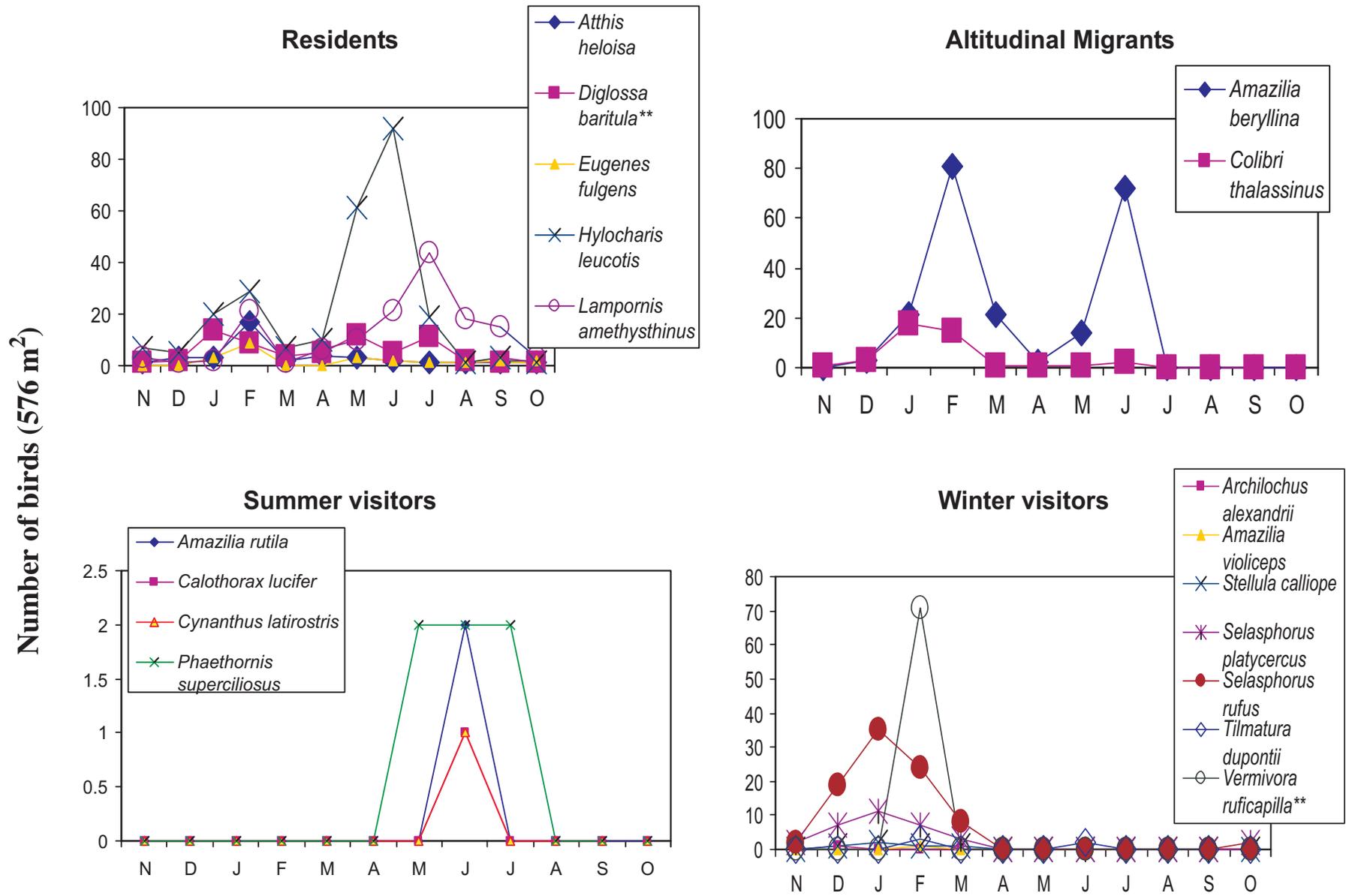
Fig. 5. Time course of the ratio of pollinators to nectar robbers in the forested area (■) and the nonforested area (+) sampled in Manantlán throughout the year (November to October).
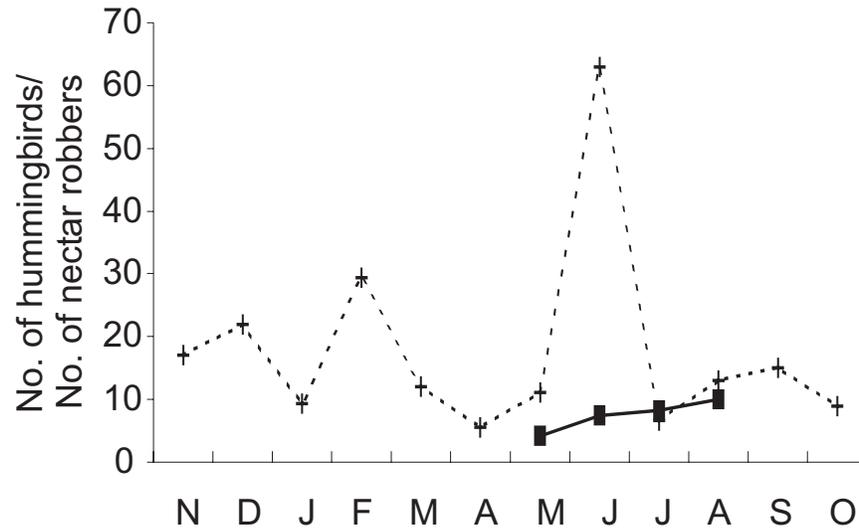

Table 2. Proportions of hummingbirds that bore pollen of a given plant species.

Plant species	Hummingbird species[a]														
	Ab	Ah	Ar	Av	Ct	Ef	Hl	La	Ps	Sp	Sr	Sc	Td	Db	Vr
N	205	38	2	1	40	24	256	145	6	28	88	5	5		
Bomarea hirtella		0.88			0.88	0	0.95	0.18	0.5					0	–
Byttneria catalpifolia		0				0	0.03	0.17		0				0	–
Calliandra grandifolia	0.33	0			0.5	0.88	0.36	0.71		0.27	0.1	0		0	–
Cestrum sp.	0				0	0.4	0.08	0		1	0.5			0	–
Cirsium jaliscoense	0.05	0.04	0.5	1	0	0.08	0.02	0.03	0	0.17	0	0	0	0	–
Crusea coccinea	0.01	0	1		1	015	0.31	0.2	0	1				–	–
Fuchsia microphyla	0.04	0.05	0.5	0	0.04	0.33	0.18	0.34	0	0.18	0.06	0	0.2	0	–
Fuchsia fulgens	0	0	0.5	0	0	0.88	0	0.24	0.5	1				0	–
Ipomoea heredifolia	0.06	0.05	0	0	0.02	0.17	0.04	0.1	0	0.04	0.05	0	0	0	–
Ipomoea orizabaensis	0.01	0		0	0	0.33	0	0		0	0	0	0	0	–
Lobelia laxiflora	0.22	0.21	1		0.18	0.29	0.45	0.12	0.17	0.32	0.08	0.2	0	0	–
Malvaviscus arboreus	0	0		0	0	0.06	0	0.03	0	0.04	0	0	0	0	–
Phaseolus coccineus	0.67	0.67			1	0.95	0.88	0.95		0.18	0.14			0	–
Psittacanthus ramiflorus	0,18	0.44	1		0.75	0.58	0.34	0.39	0.17	0.75	1		0	0	–
Salvia lavanduloides		1			1	0	0.75	0.03		1				–	–
Salvia mexicana	0.74	0.62	1	1	0.95	0.4	0.51	0.3		0.96	0.73	0.8	0.6	0	0
Salvia iodantha	0.73	0.62	1	1	0.95	0.40	0.48	0.3		0.92	0.73	0.8	0.6	0	0
Stachys aff. *liundenii*	0.25	0	1			0.13	0.01	0.11	0.5	1				–	–
Tillandsia sp.	0.05	0.05		0	0.16	0.09	0.1	0		0.14	0.08	0.33	0	0	–

Note: For nectar robbers (Db and Vr), only visited (+) and nonvisited (–) plants are indicated.

[a]Ab, *Amazilia beryllina*; Ah, *Atthis heloisa*; Ar, *Amazilia rutila*; Av, *Amazilia violiceps*; Ct, *Colibri thalassinus*; Ef, *Eugenes fulgens*; Hl, *Hylocharis leucotis*; La, *Lampornis amethysthinus*; Ps, *Phaethornis superciliosus*; Sp, *Selasphorus platycercus*; Sr, *Selasphorus rufus*; Sc, *Stellula calliope*; Td, *Tilmatura dupontii*; Db, *Diglossa baritula*; Vr, *Vermivora ruficapilla*.

piercing, and probably acts as a pollinator of this species. *Bytnneria catalpifolia*, a plant that produces small cup-shaped flowers, was visited sometimes via the correct entrance, but in other instances it was pierced. The fourth species, *P. ramiflorus*, has long tube-shaped flowers that the bird visited by perching above the inflorescence and introducing its head among the flowers to reach the base of the corolla and pierce it. In attempting to reach the inner flowers of the in-florescence, the bird may be dusted with pollen from the outer flowers and pollinate them.

Discussion

The prevalence of nectar robbing in this system is high, almost all plant species visited by hummingbirds in the area also being pierced by *D. baritula* and a mean of 85% plant

species being visited throughout the year. The results are in accordance with the idea that *D. baritula* specializes in piercing hummingbird-pollinated plants (Skutch 1954; Faegri and van der Pijl 1979).

Hummingbirds showed preferences in their seasonal use of the different plants available. Some plant species were preferred by them, such as species in the genus *Salvia*, and others were used less that expected, such as *C. coccinea*. The relationship between hummingbirds and plants of the genus *Salvia* is widely recognized (Wolf 1970; Wyatt 1983; Chavez 1999). However, *C. coccinea* has all the characteristics of a hummingbird-visited flower but was used less than expected. It produces little nectar and the sugar concentration is low compared with nectars of hummingbird-visited flowers (Baker and Baker 1975), but the caloric content of the reward is comparable to that of other plant species that were found to be more used, such as *F. microphylla*. This may be a reflection of other nectar characteristics not measured here that can influence nectar quality and have recently been discovered to be important for some plant species. However, summer visitors forage to a great extent on this plant species, but these data must be treated with caution and were not used in the analysis because of the very limited sample size.

Seasonal variation in the use of plant species was similar between resident hummingbirds and *D. baritula*. Moreover, the robber and the hummingbirds used plants with particular morphological characteristics (tubular or cup-shaped and red or orange). This stresses its degree of specialization and its "hummingbird-like" behavior, which was first recognized in 1871 (Vallada 1871) and has been accepted until now (see Faegri and van der Pijl 1979). The frequency of robbery at the individual-plant level was very variable among the plants surveyed (8.5–57.6%), and low compared with other plants studied, where damaged flowers represent around 70% of the total number of flowers per plant (Navarro 2000, 2001). This may be related not only to the relatively low abundance of robbers compared with pollinators and the high diversity and availability of nectar rewards found in this system, but also to variability among plants in the quality of the reward, which can be negatively related to frequency of robbery, as energetic requirements may be satisfied sooner when nectar is higher in quantity or sugar concentration.

Given the high overlap between the plant species visited by hummingbirds and nectar robbers, direct and indirect negative effects on hummingbirds and plants could be expected. However, the magnitude of the effects, for both the plants and the pollinators, depends on the ratio of pollinators to robbers (Soberón and Martínez del Río 1985). The results of this work show that throughout the year, hummingbirds were always more abundant than robbers, their numbers being between 5 and 60 times higher. Thus, the probability of piercing, in relation to pollination, must be rather low through time. Likewise, the probability of encounter between hummingbirds and robbers, leading to agonistic interactions and thus negative effects for both groups (Soberón and Martínez del Río 1985), must also be low.

Nectar robbers can be regarded as pollinators of some plants (Inouye 1983). Here I have documented the presence of pollen from four plant species on the robbers' bodies. It is possible that at least for these four species, *D. baritula* might act as a pollinator. The four species can be assigned to two groups according to their pollination syndrome (as defined by Faegri and van der Pijl 1979): (*i*) those bearing open flowers pollinated by a wide array of visitors, including perching birds (*C. grandifolia*, *C. jaliscoense*, and *B. catalpifolia*), and (*ii*) the vine *P. ramiflorus*, with long-tubed flowers (arranged in a dense inflorescence) in which the nectar is kept concealed in the bottom of the tube. Pollination in the latter could take place as a result of circumstantial dusting of the robber's body while it is piercing. A similar situation is reported for *Diglossa* sp. and the mistletoe *Tristerix longebracteanus* in Perú (Graves 1982). All of these plants bear their flowers in inflorescences. The clumping of flowers appears to facilitate indirect dusting of the nectar robber with pollen and, thus, pollination (Graves 1982).

The role of nectar robbers and their effects on the hummingbird pollination system must be treated with caution, as the consequences depend on a complex array of direct and indirect effects that can vary temporally and spatially (i.e., Arizmendi et al. 1996; Herrera 1996; Waser et al. 1996; Irwin and Brody 1998, 1999; Navarro 2001). In Manantlán, *D. baritula* can be regarded as a commensal of the system or simply as another hummingbird-like species that changes its behavior from a pollinator of some plants to a "cheater" of others as some other members of the guild are (Soberón and Martínez del Río 1985; Arizmendi et al. 1996). However, the effects of this robber in relation to the reproductive success of most of the plants it visits remain to be tested experimentally in order to fully understand its role in the community.

On the other hand, the role of *V. ruficapilla* in the system is clearly that of a robber that damages the flowers while visiting. However, it was detected visiting only two plant species (*S. mexicana* and *S. iodantha*) at the peak of their flowering season. It steals nectar in a way which resembles that reported by Askins et al. (1987) for other perching birds which damage the flowers of a tropical tree, having a clearly negative effect on the female fitness of the plant. This species can be treated as a migrant robber that has negative effects on female fitness in the two plant species visited, but its effects on the male fitness and on hummingbirds and *D. baritula* remain to be studied in more detail.

Acknowledgments

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