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Interacciones Ecológicas Múltiples: El caso del sistema mutualista colibríes - plantas y el ladrón de néctar _Diglossa baritula_ (Passeriformes: Aves)

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Presentación

La polinización de las plantas por colibríes ha sido reconocida como una de las interacciones biológicas en donde se han desarrollado una mayor cantidad de adaptaciones recíprocas. Este sistema ha sido usado recurrentemente como uno de los mejores ejemplos de coevolución (Brown & Kodric-Brown 1979, Faegri & van der Pijl 1979, Johnsgard 1983, Stiles 1980 1981). Las flores polinizadas por colibríes presentan colores llamativos (por ejemplo, rojos o anaranjados, etc.), una posición péndula y altas tasas de producción de néctar. Por su parte los colibríes son aves de tamaño pequeño (1.5-9 g), con picos y lenguas largas y tasas metabólicas altas (Faegri & van der Pijl 1979, Johnsgard 1983). Su alimentación se basa casi exclusivamente en néctar, aunque ocasionalmente consumen insectos (Johnsgard 1983), y son reconocidos como los polinizadores más especializados de entre las aves nectarívoras (Johnsgard 1983, Stiles 1981). Los colibríes presentan una alta dependencia de las flores productoras de néctar, lo cual se muestra en la sincronización de sus períodos reproductivos con los picos de floración, así como en los eventos migratorios que se encuentran altamente ligados a la floración secuencial que se presenta a lo largo de todo el gradiente latitudinal por donde se mueven (Johnsgard 1983, Grant & Grant 1965, Hutto 1986, Stiles 1981).

El néctar producido por las plantas parece ser una inversión costosa ya que constituye entre el 4 y el 36% del presupuesto diario de carbono de una planta (Pyke 1981, Southwick 1984). Por esta razón se ha postulado que las flores de colibríes han evolucionado hacia una forma tubular y larga para limitar el acceso sólo a los polinizadores "legítimos" (Faegri & van der Pijl 1979, Inouye 1983, Stiles 1981, Wolf & Stiles 1989). Estas flores generalmente tienen tejidos protectores alrededor de los nectarios, lo que dificulta el acceso a visitantes "ilegítimos" que perforan la corola (Faegri & van der Pijl 1979, Inouye 1983). No obstante, estas flores atraen a muchos animales que intentan obtener la recompensa, ya que el néctar es un recurso muy codiciado por ser fácil de metabolizar y proveer una gran cantidad de energía (Faegri & van der Pijl 1979, Stiles 1981).

El efecto de los ladrones de néctar sobre el sistema mutualista de polinización por colibríes es un tema muy controvertido. Dado que el néctar es un recurso costoso para la planta y una fuente de alimento indispensable para los colibríes, el efecto de un ladrón debería ser, teóricamente, negativo para ambos mutualistas. Aunque, existen trabajos en donde se apoya el argumento de que los efectos son negativos, existen otros en donde se dice que son positivos, es decir que los ladrones polinizan, y otros en donde se les considera neutros (Inouye 1983). El propósito de este trabajo es conocer cuál es el efecto del ladrón de néctar <u>Diglossa</u> <u>baritula</u> (Passeriformes: Aves) sobre el sistema plantas-colibríes en un bosque húmedo de montaña en el oeste de México. Como preámbulo a este estudio, se presenta en primer lugar una revisión detallada sobre lo que es conocido acerca de la importancia y efectos de los ladrones de néctar sobre los sistemas de polinización biótica (Capítulo I).

En el caso particular del sistema de estudio de la presente tesis, este efecto se midió a varios niveles, comenzando con una evaluación de la prevalencia del robo asi como de la dinámica temporal de cada uno de los componentes del sistema, dado que se sabe que el efecto de los ladrones de néctar medido sobre la producción de semillas de las plantas depende en parte de las abundancias de ladrones y polinizadores y de su variación temporal (ya que de esto depende la frecuencia de visita de polinizadores y ladrones a una flor, Capítulo II). En segundo lugar, se investigó en detalle la historia natural de Diglossa baritula estudiando en condiciones naturales i) la frecuencia y prevalencia del daño floral entre las plantas polinizadas por colibríes y su variación temporal ii) la identidad, características y producción de flores de las plantas visitadas por el ladrón y iii)los efectos en condiciones naturales del robo de néctar sobre la producción de semillas de dos especies de plantas (Capítulo III).

Por último, y de manera experimental, se evaluó el efecto del ladrón sobre la producción de néctar y semillas de dos especies de plantas polinizadas por colibríes (Fuchsia microphylla y Salvia mexicana, Capítulo IV). Tomando en cuenta que la eficiencia de los polinizadores es variable (Cruden 1972, Horvitz & Schemske 1984, Jenersten & Morse 1991, Primack & Selander 1975, Schemske & Horvitz 1984) en este experimento se evaluó la eficiencia de diferentes visitantes florales en la producción de semillas de las plantas.

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Capítulo I

Antecedentes: los ladrones de néctar, su importancia y sus efectos sobre los sistemas de polinización biótica.

La interacción ecológica entre plantas y los colibríes que las polinizan ha sido usada como modelo de sistemas muy especializados, en donde plantas y colibríes han desarrollado adaptaciones morfológicas y fisiológicas para que se dé la interacción (Stiles 1981). De esta forma, es ampliamente reconocido que las flores de las plantas polinizadas por colibríes presentan ciertas características que permiten que se las puedan reconocer como un grupo. Estas características constituyen lo que se conoce como el síndrome de ornitofilia (Faegri & van der Pijl 1979, Stiles 1981). Las flores de las plantas polinizadas por colibríes presentan forma tubular y colores llamativos, generalmente cercanos a la gama del rojo. Su posición es generalmente péndula y secretan néctar en grandes cantidades, aunque con concentraciones moderadas de azúcares (Baker & Baker 1975, Pyke & Waser 1981, Stiles 1981).

Los colibríes son aves de tamaño pequeño (1.5-9 g), con picos y lenguas largas y delgadas y con capacidad de revolotear (Johnsgard 1983, Stiles 1981). Este sistema ha sido tomado como uno de los mejores ejemplos de coevolución en donde ambos grupos presentan adaptaciones mutuas de notable correspondencia (véase p.ej. Kodric-Brown & Brown 1979, Stiles 1981).

Desde el punto de vista fisiológico, los colibríes son, de entre las aves, los que presentan metabolismos más acelerados (Heinrich & Raven 1972, Johnsgard 1983, Stiles 1981), por lo que requieren un alimento que esté presente en grandes cantidades y que les suministre energía de manera eficiente. Como se dijo anteriormente, las flores polinizadas por colibríes producen grandes cantidades de néctar. El néctar es una mezcla de azúcares (glucosa, fructuosa y sacarosa) y agua y por lo tanto representa un alimento fácil y rápido de digerir (Heinrich & Raven 1972). Estas flores presentan por lo general tejidos protectores que rodean a los nectarios cuya función es evitar la visita de "intrusos" que tomen la recompensa sin polinizar restringiendo el acceso al néctar sólo a los polinizadores legítimos (Johnsgard 1983, Inouye 1983, Stiles 1981).

El néctar es además una recompensa "costosa" para la planta. Se ha calculado, para Asclepias syriaca, que la secreción de néctar consume entre 4 y 36.6% del total del fotosintato diario producido por la planta (Southwick 1984). Para la alfalfa (Medicago sativa), la producción de néctar representa el doble de la energía dedicada a la producción de semillas (Southwick 1984), mientras que Senecio vulgaris dedica entre 3 y 5% de la energía total producida para elaborar el néctar (Harper & Ogden 1970).

Por otra parte, se ha visto que la calidad y la cantidad de néctar producido por una planta afecta la cantidad y "calidad" (en términos de la eficiencia de los visitantes) de las visitas recibidas (Heinrich & Raven 1972, Mitchell 1991, Pyke 1981, Schemske & Horvitz 1984, Southwick 1984, Stiles 1981) y, por lo tanto, la eficiencia en la polinización.

El patrón de producción de néctar característico de las flores de colibríes, aunado al alto valor energético que representa el néctar para los animales, hacen a estas flores "codiciadas" entre numerosos grupos de animales que intentan obtener la recompensa, pero que debido a limitaciones morfológicas o fisiológicas no pueden hacerlo utilizando la entrada "correcta". De esta forma, muchos de estos animales obtienen el néctar perforando las corolas de las flores, con lo que se llevan la recompensa sin polinizar. A estos animales, se les ha llamado ladrones de néctar (Inouye 1983). Además, se sabe que las especies de polinizadores que visitan una especie de planta, difieren entre sí en su eficiencia para polinizar, existiendo polinizadores muy eficientes, también llamados primarios, y poco eficientes o secundarios (Schemske & Horvitz 1984, Wolf & Stiles 1989). En ocasiones, algunos animales que visitan por la entrada correcta, no transportan el polen de la planta y por lo tanto podrían catalogarse como ladrones.

De esta forma, los sistemas mutualistas de polinización por colibríes, están rodeados de una gran cantidad de "visitantes", al igual que en el caso de otros mutualismos considerados también como especializados, como en las plantas que producen nectarios extraflorales y las hormigas que las protegen de herbívoros (Horvitz & Schemske 1984). Los efectos de estos visitantes florales para ambos mutualistas se conocen poco (Heinrich & Raven 1972, Inouye 1983).

El estudio de las interacciones planta-animal, considerando los diferentes visitantes que ocurren en un solo sistema, así como sus consecuencias sobre la adecuación de los interactuantes, es indispensable para entender los procesos demográficos y evolutivos que operan en el sistema (Horvitz & Schemske 1984). Por ejemplo, se ha visto que muchos mutualismos de polinización han evolucionado en presencia de un tercer taxón que opera de manera negativa sobre uno de los mutualistas (Heithaus **et al.** 1980). Un ejemplo es la herbivoría, la cual es una fuerza negativa que ha favorecido la producción de néctares extraflorales que atraen hormigas, que a su vez atacan a los herbívoros (Price **et al.** 1980), protegiendo a las plantas de sus consumidores.

LOS LADRONES DE NÉCTAR

Los ladrones de néctar son animales cuya presencia en las flores y por lo tanto en los mutualismos como la polinización biótica debe ser común y frecuente (Heinrich & Raven 1972, Inouye 1983). Acerca de este tema se ha escrito relativamente poco, aunque se conoce un total de 112 especies de plantas en las que se ha documentado robo de néctar (Tabla 1.1), (pertenecientes a 43 familias) con 112 especies de animales descritas como ladrones de néctar. La información conocida se resume en el Apéndice 1.1. Las familias de plantas con más especies visitadas por ladrones de néctar son Scrophulariaceae y Leguminosae (de las que el 65% son Papilionoideae) con once especies cada una, y Labiatae, con seis (Tabla 1). Es notorio que las familias con muchas especies no son en todos los casos las que presentan mayores números de especies reportadas como robadas. Por ejemplo, la familia Rubiaceae tiene 6500 especies mientras que Eleagnaceae tiene 50 y ambas presentan sólo una especie hasta ahora descrita como robada. Al parecer el número de especies documentadas como robadas, por familia es independiente de la riqueza específica de cada familia. No obstante es de hacer notar que en ausencia de muestreos sistemáticos de la incidencia de robo, estas tendencias deben considerarse con cautela.

Los polinizadores más frecuentes de las plantas que experimentan robos son abejas (28%), colibríes (23%), y aves percheras (20%) (Fig. 1.1).

Los ladrones de néctar más numerosos son los himenópteros, principalmente abejas carpinteras y abejorros, seguidos por aves percheras, colibríes y hormigas (Fig. 1.1). El número promedio de especies de ladrón por especie de planta es 4.35 (DE= 2.34, rango 1-10). El valor modal del número de especies de ladrón por planta es, notablemente, de 1 (46% de los casos). Esto sugiere que aunque una proporción considerable de las especies son robadas por una sola especie de ladrón, hay mucha varianza al grado de que especies como Impatiens capensis (Balsaminaceae) reciben hasta 10 especies de ladrones.

El análisis de la muestra conocida,revela que la interacción con ladrones de néctar está bien difundida en los sistemas de polinización, estando representado en un número grande de familias de plantas aunque en pocas especies. De cualquier forma, existen pocas publicaciones al respecto (66; ver Apéndice 1.1), lo que nos da una idea de lo poco que se ha estudiado este fenómeno, aunque

Tabla 1.1. Familias de plantas en las que se han encontrado especies robadas y número de especies robadas y total de cada familia. Las denominaciones familiares se tomaron de Cronquist (1981).

Familia	Numero Especies Robadas	Numero Total de Especies
Hostaceae	2	12
Eleagnaceae	1	50
Cannaceae	2	50
Convallariaceae	1	70
Tropaeolaceae	1	92
Asphodelaceae	1	120
Costaceae	1	150
Papaveraceae	1	200
Bombacaceae	2	200
Polemoniaceae	1	300
Nyctaginaceae	1	300
Podocarpaceae	1	300
Grossulariaceae	1	350
Plumbaginaceae	1	400
Caprifoliaceae	4	400
Balsaminaceae	4	450
Hyacinthaceae	1	500
Dracaenaceae	1	600
Agavaceae	4	600
Passifloraceae	1	650
Onagraceae	2	675
Loranthaceae	1	700
Araliaceae	1	700
Aloaceae	1	700
Bignoniaceae	3	800
Gentianaceae	1	1000
Ranunculaceae	3	1000

Iridaceae	1	1500
Malvaceae	4	1500
Convolvulaceae	5	1500
Asclepiadaceae	1	2000
Caryophyllaceae	1	2000
Campanulaceae	2	2000
Apocynaceae	3	2000
Boraginaceae	4	2000
Acanthaceae	5	2500
Verbenaceae	2	2600
Solanaceae	3	2800
Labiatae	6	3200
Ericaceae	5	3500
Scrophulariaceae	11	4000
Rubiaceae	1	6500
Leguminosae	11	14000
Total	109	64969

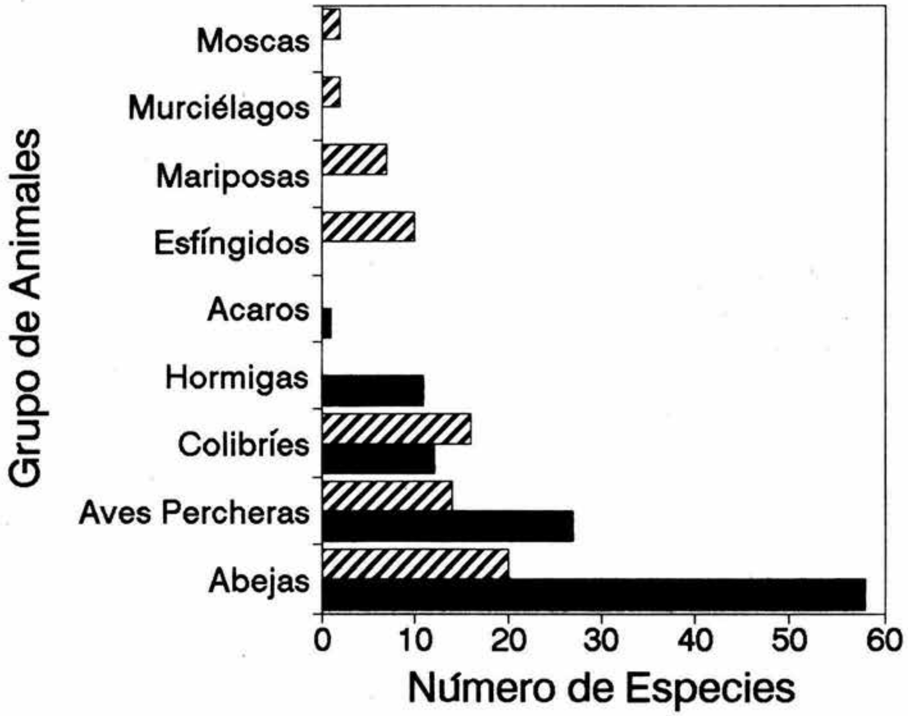

FIGURA 1.1 Grupos de animales que han sido encontrados como polinizadores (barras achuradas) o como ladrones de néctar (barras sólidas) de las plantas que experimentan robos.

para cualquiera que observe flores en la naturaleza, la presencia de ladrones de néctar resulta evidente y probablemente mucho más común de lo que la información disponible sugiere.

EL PAPEL DE LOS LADRONES DE NÉCTAR EN LOS SISTEMAS DE POLINIZACION BIOTICA

El efecto de los ladrones de néctar sobre las plantas y sus polinizadores debería ser negativo si consideramos que 1) la producción de néctar representa un costo para las plantas, y al ser el néctar una recompensa "cara" y 2) de la misma forma, para los colibríes, que son animales de alto metabolismo (y que por lo tanto requieren de grandes cantidades de energía para poder sobrevivir), al encontrar flores robadas y por lo tanto con menores cantidades de néctar, tendrán que aumentar el número de flores visitadas para nivelar sus requerimientos energéticos. Los efectos negativos pueden darse si el polinizador y el ladrón interactúan directamente y de forma negativa, de manera que el polinizador sólo visite flores sin robo. O bien si aún cuando ambos visitan las mismas flores, el polinizador o la planta obtienen menos recursos o polinizaciones, respectivamente. Roubick (1982) encontró que la abeja Trigona ferricauda perfora la corola de Pavonia dasypetala y observó interacciones agresivas entre esta abeja y el polinizador de la planta, el colibrí Phaethornis superciliosus. En estas interacciones la abeja excluye por completo al polinizador. Experimentalmente, Roubick (1982) encontró que las flores que habían sido perforadas sufrían una reducción significativa en el número de frutos producidos con respecto a las flores solamente visitadas por el polinizador. Colwell (1973) y Colwell **et al.** (1974) estudiando a Centropogon valerii encontraron que el polinizador (Colibri thalassinus) y el ladrón de néctar (Diglossa plumbea) no interactúan agresivamente y que al parecer existe una repartición espacial de las flores de los arbustos entre estos dos animales. El colibrí usa las flores altas y externas y el ladrón las flores internas e inferiores. Sin embargo no se estudió el efecto sobre la producción de semillas de la planta. En Justicia aurea y Aphelandra golfodulcensis, ambas polinizadas por colibríes, existe una reducción significativa en el número de semillas producidas por flores dañadas, en comparación con aquellas intactas. También se detectó una disminución en la producción de néctar debido a los ladrones (McDade & Kinsman 1980).

Por otro lado, hay autores que piensan que los ladrones pueden actuar como polinizadores y por lo tanto tener efectos positivos sobre las plantas (Macior 1966, Koeman-Kwak 1973, Graves 1982, Stiles 1992), teniendo entonces que ser considerados mutualistas. Otros autores piensan que los ladrones en realidad son comensales y sus "efectos" son neutros sobre el sistema. Los "efectos neutros" o la ausencia de efecto pueden ocurrir cuando el ladrón no daña los tejidos reproductivos de la planta al tomar el néctar y/o no reduce el éxito reproductivo de la misma. Para los polinizadores el efecto sería neutro si la cantidad de néctar fuera ilimitada, de manera que no existiera competencia por este recurso (Inouye 1983).

En realidad, la interacción entre los ladrones de néctar y los sistemas de polinización no solo depende de la dirección (signo) de los efectos sobre los interactuantes sino también de la abundancia y variación estacional de los componentes de los sistemas (plantas-polinizadores-ladrones), tal como lo muestran los modelos matemáticos propuestos para predecir el crecimiento poblacional bajo interacciones como depredación y competencia (Krebs 1978), y para sistemas mutualistas en presencia de ladrones (Soberón & Martínez del Río 1985). En estos modelos el crecimiento de una especie, cuando ocurre la interacción, depende de 1) la tasa intrínseca de crecimiento propia, 2) de la densidad de la especie con la que se interactúa y 3) de la capacidad competitiva o eficiencia de la otra.

En este sentido el sistema de polinización biótica en presencia de ladrones de néctar podría mantenerse estable si los polinizadores están siempre en números muy por encima de los ladrones, ya que con esto se aseguraría una mayor proporción de visitas por los polinizadores en relación con los ladrones. Esto mantendría baja: 1) la tasa de robo en relación con la de polinización, 2) la probabilidad de encuentro ladrón-polinizador, disminuyendo la intensidad de la competencia por el recurso entre ambos grupos y 3) la proporción de flores con poco o ningún néctar (Soberón & Martínez del Río 1985). Aunado a esto, la eficiencia del polinizador y del ladrón, y el grado de daño que produce éste sobre el sistema (i.e. para la planta si el ladrón daña los órganos reproductivos y para los polinizadores la cantidad de néctar que los ladrones consumen), influirían en el resultado de la interacción. Dependiendo de la intensidad de estos efectos, y de su constancia temporal, las consecuencias podrían trascender del plano ecológico al evolutivo.

De esta forma, no sólo es importante conocer el efecto de los ladrones de néctar sobre el sistema (medido como cambios en la adecuación), sino también conocer su variación temporal en cuanto a composición específica y, junto con ésto, las fluctuaciones en las abundancias de todos los integrantes del sistema (plantas, polinizadores y ladrones).

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Apéndice 1.1

Recopilación de la información conocida sobre plantas polinizadas bioticamente que son visitadas por ladrones de néctar. El tipo de polinizador se refiere a primario (I) o secundario (II); El tipo de ladrón es P primario; S secundario; * visitante ilegítimo; ** desconocido (ver texto).

Especie	Polinizador (Tipo)	Ladron (Tipo)	Fuente
Abutilon sp.		*Xylocopa sp. (P)* *Parus tenerife (P)*	Muller (1895) Oldnam (1896)
Agave salmiana	*Icterus galbula (II)* Murcielagos (I) *Icterus parisorum (II)* *Diglossa baritula (II)* *Melanotis coerulescens (II)* *Colaptes auratus* *Toxostoma curvirostre*	*Amazilia beryllina (*)* *Eugenes fulgens (*)* *Hylocharis leucotis (*)* *Amazilia violiceps (*)* *Lampornis clemenciae (*)*	Martinez del Río et al. (1989)
Agave schotii	Abejas (I) Abejorros (I)	*Crematogaster dentinodus (P)* *Forelius pruinosus (P)*	Schafler et al. (1983)
Allamanda oenotheraefolia		*Xylocopa sonorina (P)*	Nishida (1963)
Aloe vera		*Sylvia atricapilla (P)* *Phylloscopus fortunatus (S)*	Oldnam (1896)
Amsonia tabernaemontana		*Xylocopa sonorina (P)*	Pammel (1888)
Anisacanthus quadrifidus		*Xylocopa sp. (P)*	Janzen (1964)
Antholyza aethiopica		*Sylvia simplex (P)*	Oldnam (1896)
Antirrhinum linaria		*Xylocopa violacea (P)*	Kirbi & Spence (1846)
Antirrhinum majus		*Xylocopa violacea (P)*	Kirbi & Spence (1846)
Aphelandra golfodulcensis	*Phaethornis superciliosus (I)* *Phaethornis longuemareus (I)* *Heliotrix barroti (I)*	*Xylocopa sp.* *Trigona sp. (P)* *Heliotrix barroti (S)* *Phaethornis longuemareus (S)* *Thalurania furcata (S)* *Coereba flabeola (P)* *Amazilia tzacatl (S)*	McDade et al (1980)
Aquilegia sp.		*Apis mellifera (S)* *Bombus sp. (P)* *Lasioglossum (S)*	Macior (1966)
Aquilegia vulgaris		*Bombus terrestris (P)* *Xylocopa virginica (P)* *Apis mellifera (S)*	Pammel (1888)
Asclepias syriaca	Mariposas (I)	*Lasius neoniger (P)* *Tapinoma sessile (P)*	Fritz et al. (1981)
Asystasia gangetica		*Xylocopa sonorina (P)* *Apis mellifera (S)*	Barrows (1980)
Azalea sp.		*Xylocopa virginica (P)*	Weiss & Smith (1940)
Brachyotum lindenii	*Metallura williami (I)* *Lesbia victoriae (I)* *Diglossa humeralis (I)* *Diglossa lafresyani (I)*	*Bombus sp (P)*	Stiles, et al (1992)
Canna indica		*Xylocopa violacea (P)*	Pammel (1880)
Canna indica var. orientalis		*Cinnyris chalybaeus (P)*	Swynnerton et al. (1916)

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Castilleja irasuensis	*Selasphorus flammula (I)*	*Diglossa plumbea (P)*	Wolf et al. (1976)
Cavendishia smithi	*Lampornis castaneoventris (II)* *Panterpe insignis (I)*	*Diglossa plumbea (P)*	Wolf et al. (1976)
Cavendishia sp.	*Lampornis castaneoventris (I)* *Panterpe insignis (I)*	*Diglossa plumbea (P)*	Wolf et al. (1976)
Ceiba acuminata	*Leptonycteris sanborni (I)* *Erriba sp. (I)* *Amazilia rutila (II)*	*Bombus sp. (*)* *Phaethornis longuemareus (*)* *Icterus pustullatus (*)* *Cacicus melanicterus (*)* *Centris sp. (*)* *Apis mellifera (*)*	Baker et al. (1971)
Centropogon thalamancensis	*Eugenes fulgens (I)*	*Diglossa plumbea (P)* *Bombus sp (S)* *Diglossa plumbea (P)*	Wolf et al. (1976) OTS (1988)
Centropogon valerii	*Colibri thalassinus (I)* *Panterpe insignis (II)* *Colibri thalassinus (II)* *Eugenes fulgens (II)* *Panterpe insignis (II)*	*Diglossa plumbea (P)* *Rhinoseius colwelli (**)* *Selasphorus flammula (S)* *Diglossa plumbea (P)* *Bombus sp (s)*	Wolf et al. (1976) OTS; Colwell (1974)
Centrosema pubescens		*Xylocopa confusa (P)*	van der Pijl (1954)
Cestrum sp.	*Panterpe insignis (I)* *Lampornis castaneoventris (II)*	*Diglossa plumbea (P)*	Wolf et al. (1976)
Cherodendron molle		*Xylocopa darwini (P)*	Linsley et al. (1966)
Convallaria polygonatum		*Apis mellifera (S)* *Bombus mastrucatus (P)* Avispa ichneumonida (S)	Pammel (1888)
Convolvulus sp.		*Xylocopa sonorina (P)*	Williams (1926, 1927)
Cordia myxa		*Xylocopa violacea*	Pammel (1880)
Costus speciosus		*Xylocopa sp. (P)*	van der Pijl (1954)
Crescentia alata	*Glossophaga soricina (I)*	*Trigona fulviventris (P)*	Martinez del Rio &
Datura stramonium		*Emphoropsis laboriosus (P)*	Nunez-Farfan 1993 Bullock (1990)
Delphinium sp		*Xylocopa sp. (P)*	Parthasarthy Iyengar 1923
Dicentra spectabilis		*Bombus jonelus (S)* *Bombus terrestris (P* *Bombus pratorum (P)* *Apis mellifera (S)* *Megachile centuncularis (S)* *Osnia rufa (S)* *Bombus ruderarius (P)* *Bombus lucorum (P)*	Pammel (1888)
Diervilla caraeensis		*Xylocopa appendiculata (P)*	Miyamoto (1961)
Diervilla florida		*Xylocopa virginica (P)*	Burrill (1925)
Diervilla japonica		*Xylocopa virginica (P)*	Pammell (1888)
Digitalis purpurea		*Xylocopa (Alloxylocopa) (P)*	Iwata (1963)
Digitalis sp.	*Panterpe insignis (I)*	*Diglossa plumbea (P)*	OTS (1988)
Disterigma humboldtii	*Centris gravisa (I)*	*Diglossa duidae (P)*	Renner (1989)
Dracaena fragans		*Cinnyris olivacina (P)*	Swynnerton et al. (1916)
Eleagnus multiflora		*Apis mellifera (S)*	Schafler et al. (1983)
Erythrina humeana		*Colius striatus (P)*	Swynnerton et al. (1916)

		Pycnonotus layardi (P)	
		Chalcomitra kirki (P)	
		Hyphantornis jamesoni (P)	
		Coliopasser ardens (P)	
		Zoosterops anderssoni (P)	
		Chalcomitra gutturalis (P)	
		Cinnyris venustus (P)	
		Cyanomitra kirki (P)	
Erythrina tomentosa		*Cinnyris chalybaeus (P)*	**Swynnerton et al. (1916)**
		Pycnonotus layardy (P)	
		Sylvia simplex (P)	
		Prinia mystaceae (P)	
		Hyphantornis jamensoni (P)	
		Sitagra jamesoni (P)	
		Coliopasser ardens (P)	
		Nectarinia artun (P)	
		Estrilda kilimensis (P)	
Falcata japonica		*Xylocopa appendiculata (P)*	**Miyamoto (1961)**
Frasera speciosa	*Bombus centralis (I)*	*Formica neorufibarba (P)*	**Norment (1988)**
	Ctenicerca fallax (I)		
	Euxoa lewisi (I)		
	Bombus frigidus (I)		
	Eulaemus synthridis (I)		
	Moscas (I)		
Fuchsia lycoides	*Rhodopsis vesper (I)*	*Rhodopsis vesper (P)*	**Atssatt & Rundell (1982)**
Galeopsis speciosa		*Xylocopa valga (P)*	**Schremmer (1953)**
Gardenia tigrina		*Phyllostrophorus milanjensis*	**Swynnerton et al. (1916)**
Gossypium barbadense		*Cinnyris venustus (P)*	**Swynnerton et al. (1916)**
		Cinnyris chalibaeus (P)	
		P. favistriatus (P)	**El-Borollosy & Ismail (1972)**
		Xylocopa pubescens (P)	
Hibiscus rosa-sinensis		*Xylocopa sp.*	**Barrows (1980)**
		Sylvia atricapilla (P)	**Oldnam (1896)**
Hosta sieboldiana		*Xylocopa appendiculata (P)*	**Miyamoto (1961)**
Hosta undulata		*Xylocopa appendiculata (P)*	**Miyamoto (1961)**
Hyacinthus sp		*Xylocopa violaceae (P)*	**Pammel (1880)**
Impatiens balsamina		*Xylocopa virginica (P)*	**Barrows (1980)**
Impatiens capensis	*Vespula melifera (II)*	*Auglochlora pura (SP)*	**Rust (1977)**
	Bombus vagans (I)	*Vespula melifera (P)*	
	Bombus impatiens (I)	*Crematogaster sp. (S)*	
	Apis melifera (I)	*Bombus affinis (P)*	
		Apis melifera (S)	
		Auglochloropsis metalica (SP)	
		Lasioglosus sp (S)	
	Bombus vagans (I)	*Bombus affinis (P)*	**Zimmerman & Cook (1985**
	Archilochus colubris (I)	*Appis mellifera (S)*	
	Bombus impatiens (I)	*Vespula maculifrons (P)*	
Impatiens pallida	*Bombus impatiens (I)*	*Auglochloropsis metalica (SP)*	**Rust (1977)**
	Bombus vagans (I)	*Bombus terricola (P)*	
		Rhiganasica (S)	
		Bombus vagans (SP)	
		Auglochlora pura (SP)	
		Bombus fervidus (P)	

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Impatiens texturi		*Bombus vagans (P)*	Miyamoto (1961)
Ipomoea nil		*Xylocopa sp. (P)*	van der Pijl (1954)
		Xylocopa mordax (P)	Free (1975)
Ipomoea crassicaulis		*Bombus sp. (P)*	van der Pijl (1954)
Ipomoea purpurea		*Xylocopa arizonensis (P)*	Cockerell (1900)
Ipomoea sp.		*Bombus sp. (P)*	Nishida (1963)
Jacaranda sp		*Xylocopa sp. (P)*	Muller, 1895
Justicia aurea	*Phaethornis superciliosus (I)*	*Phaethornis longuemareus (S)*	McDade et al. (1980)
	Glaucis aenea (I)	Hormigas	
	Phaethornis longuemareus (I)		
	Phaethornis superciliosus (I)	*Phaethornis longuemareus (P)*	Willmer & Corbet (1981)
	Campylopterus hemileucurus (I)	*Trigona ferricauda (S)*	
	Amazilia tzacatl (I)	*Trigona jaty (P)*	
		Trigona testacea (S)	
		Neoponera sp. (S)	
		Trigona fulviventris (P)	
		Ectatoma tuberculatum (S)	
		Ectatomma ruidum (SP)	
Kniphofia rhodesiana	*Chlorophoneus olivaceus (I)*	*Chlorophoneus olivaceus (P)*	Swynnerton et al. (1916)
	Cinnyris chalibaeus (I)	*Cinnyris chalibaeus (P)*	
	Pycnonotus layardi (I)	*Xylocopa sp. (PS)*	
		Pycnonotus layardi (P)	
Lamium album		*Bombus mastrucatus (P)*	Pammel (1888)
		Osnis rufa (S)	
		Apis mellifera (S)	
		Avispa ichneumonida (S)	
		Bombus terrestris (P)	
		Bombus alticola (P)	
		Apis mellifera (S)	
Lantana camara	*Danaus gilppus (I)*	*Trigona fulviventris (P)*	Barrows (1976)
	Danaus plexipus (I)		
	Eurema daira (I)		
	Urbanus sp. (I)		
	Lycorca ceres (I)		
	Anartia fatima (I)		
	Agraulis vanillae (I)		
	Anartia jathrophae (I)		
	Pierido (II)		
	Hesperido (II)		
Leonotis mollissina	*Cinnyris kirki (I)*	*Pycnonotus layardi (P)*	Swynnerton et al. (1916)
	Papilo dardanius (I)	*Cinnyris olivacina (P)*	
		Zoosterops anderssoni (P)	
		Cinnyris kirki (P)	
Linaria vulgaris		*Xylocopa sp. (P)*	Pammel (1880)
Lonicera japonica		*Xylocopa virginica (P)*	Rau (1926) Barrows (1980)
Macleania glabra	*Panterpe insignis (I)*	*Diglossa plumbea (P)*	Wolf et al. (1976)
***Manfreda** brachystachya*	Mariposas (I)	Moscas (S)	Eguiarte & Burquez
	Saturnidos (I)	*Apis mellifera (PS)*	(1987)
	Noctuidos (I)	*Carpodacus mexicanus (P)*	
	Esfingidos (I)		
	Eugenes fulgens (I)		
	Calothorax lucifer (I)		
	Hylocharis leucotis (I)		

	Cynanthus latirostris (I) *Amazilia beryllina (I)* *Leptonycteris sanborni (I)* *Leptonycteris nivalis (I)* *Anoura geoffroyi (I)*		
Melampyrum pratense		*Bombus terrestris* *Bombus lapidarius (P)* *Apis mellifera (S)*	Pammel (1888)
Melampyrum nemorosum		*Psithyrus rupestris (P)* *Apis mellifera (S)* *Bombus muscorum (P)* *Bombus lapidarius (P)* *Bombus terrestris (P)*	Pammel (1888)
Mimulus cardinalis		*Xylocopa sp. (P)*	Grant & Grant (1968)
Mirabilis jalapa	*Sphynx instar (II)* *Hylex lineata (I)* *Erynnys ello (I)* *Agrius cingulatus (II)*	*Xylocopa tabaniformis (P)* *Xylocopa tabaniformis (P)*	Kirbi & Spence (1846) Janzen (1964) Martinez del Rio & Burquez (1988)
Nolina galapagensis		*Xylocopa darwini (P)*	Linsley et al. (1966)
Passiflora vitifolia	*Phaethornis superciliosus (I)*	*Trigona sylvestriana (P)* *Trigona fulviventris (P)* Hormigas (PS)	Gill et al. (1982)
Pavonia dasypetala	*Phaethornis superciliosus (I)*	*Trigona franki (S)* *Trigona fulviventris (S)* *Trigona sylvestrana (SP)* *Trigona corvina (S)* *Trigona buyssoni (S)* *Trigona ferricauda (P)*	Roubick (1988)
Pedicularis palustris	*Bombus hortum (I)* *Bombus pascorum (I)* *Bombus muscorus (I)*	*Bombus lucorum (P)* *Bombus terrestris (P)* *Bombus jonelus (P)*	Koeman-kwak (1973)
Penstemon kunthii	*Lampornis clemenciae (I)* *Hylocharis leucotis (I)* *Eugenes fulgens (I)*	*Diglossa baritula (P)* *Bombus pulcher (S)* *Bombus trinomiatus (S)*	Lyon et al. (1971)
Petunia sp.		*Xylocopa sp. (P)*	Mann (1882)
Plumbago capensis		*Xylocopa virginica (P)*	Barrows (1980) Murtfedt (1882)
Polemonium viscosum	*Delia sp. (I)* *Bombus kirbyellus (I)* *Bombus sylvicola (I)* Halictidae (I) Andrenidae (I) *Hylex lineata (I)*	*Formica neorufibarba (P)*	Galen (1983)
Pseudobombax ellipticum	*Leptonycteris sanbornii (I)* *Icterus wagleri (II)* *Glossofaga leachii (I)* *Icterus pustulatus (II)* *Choeromycteris mexicana (I)* *Icterus galbula (II)*	*Amazilia violiceps (*)* Abejas (*) *Cynanthus sordidus (*)*	Eguiarte et al. (1987)
Psittacanthus montis-neblinae	*Campylopterus duidae (I)*	*Diglossa duidae (P)*	Renner (1989)

Apéndice 1.1

Ribes sanguineum	*Parus caeruleus (I)*	*Parus caeruleus (P)*	Swynnerton et al. (1916)
Salvia menthaefolia		*Xylocopa violacea (P)*	Pammel (1880)
Salvia pratense		*Bombus terrestris (P)* *Megachile centricularis (S)*	Pammel (1888)
Salvia sp.		*Xylocopa sp. (P)*	Leach (1921)
Saponaria officinalis		*Xylocopa virginica (P)*	Barrows (1980)
Saritaea magnifica		*Xylocopa latipes (P)*	van der Pijl (1954)
Sophora angustifolia		*Xylocopa appendiculata (P)*	Miyamoto (1961)
Stachytarpheta sp.		*Xylocoopa sonorina (P)*	Barrows (1980)
Symphytum officinale		*Megachile centricularis (S)* *Bombus terrestris (P)*	Pammel (1888)
Symphytum peregrinum		*Bombus pratorum (P)* *Anthidium manicatum (S)*	Pammel (1888)
Symphytum tuberosum		*Xylocopa violacea (P)*	Pammel (1880)
Thevetia peruviana		*Xylocopa sonorina (P)*	Barrows (1980)
Thunbergia erecta		*Xylocopa sonorina (P)*	Nishida (1963)
Trifolium pratense		*Bombus lucorum (P)* *Apis mellifera (S)*	Hawkins (1961)
Tropaeolum lobbianum		*Xylocopa violacea (P)*	Pammel (1880)
Vaccinium consanguineum	*Selsaphorus flamula (I)* *Panterpe insignis (II)*	*Diglossa plumbea (P)*	Wolf et al. (1976)
Vaccinum corymbosum		*Xylocopa virginica (P)*	Dorr & Martin (1966)
Vereia crenata		*Coereba flabeola (P)*	Moore (1878)
Vicia faba		*Xylocopa pubescens (P)* *Bombus terrestris (P)* *Bombus mastrucatus (P)* *Osnia rufa (S)* *Apis mellifera (S)* Avispa ichneumonida (S)	El-Borollosy & Ismail (1972) Pammel (1888)
Vicia sepium		*Bombus terrestris (P)* *Osnia rufa (S)* *Bombus mastrucatus (P)* *Apis mellifera (S)* Avispa ichneumonida (S)	Pammel (1888)
Vicia villosa		*Halictus sp. (S)* *Apis mellifera (S)* *Bombus terrestris (P)* *Lassioglossum sp. (S)* *Andrena sp. (S)* *Xylocopa sp. (P)*	Benedeck et al. (1973) Weaver (1956); Benedek et al. (1973)
Wisteria sinensis		*Xylocopa virginica (P)*	Gentry (1875)
Zauschneria californica		*Xylocopa sp. (P)*	Grant & Grant (1968)

Capítulo II. Un estudio de caso de interacciones ecológicas múltiples: los colibríes, las plantas y las aves ladronas de néctar en un bosque alto en México.

A study case of multiple ecological interactions: hummingbirds, plants, and avian nectar robbers in a highland forest in Mexico.

Abstract

Nectar robbers are animals that extract the nectar produced by plants, as a reward for their legitimate pollinators, without producing any service as pollinators. The effect of nectar robbery, wether negative, neutral or positive, depends in part on the relative abundance of pollinators and robbers, as probabilities of both flower piercing and agonistic encounters with pollinators vary as this ratio changes. The purpose of this study is to provide a general description of the temporal (throughout a year) and spatial (on two contrasting vegetation areas) dynamics of i) flower availability ii) their use by hummingbird pollinators and iii) nectar robbers. This is a first step to assess the role of nectar robbers on a plant-hummingbird pollination system. The study was carried out on a tropical montane forest, previously unexplored for this mutualistic system.

The guild consisted of 17 species of hummingbirds, two nectar robbers and 21 plant species visited by nectarivorous birds. Both, abundance of birds and flowers showed two peaks, one in winter and the other in the rainy season. Hummingbird abundance varied considerably throughout the year both in number of individuals and in number of species. Eight species of hummingbirds and the nectar robber <u>Diglossa</u> <u>baritula</u> visited flowers in the two vegetation areas, all of them being more abundant in the non-forested area where the other nine species of hummingbirds were exclusively found. However, there were no statistical differences in the number of flowers in each vegetation areas throughout the year. There was a low specificity among pollinators in terms of the flowering species visited, yet, some plant species were used more than expected by their abundances. Overlap in the use of flowers among hummingbirds was high, and also between hummingbirds and the nectar robber. Plants also shared pollinators among them, both interactuants being generalists. Nectar robbery was found to be a widespread phenomenon, occurring in almost all the plants detected as hummingbird-pollinated. However, the ratio hummingbirds/nectar robbers always ranged between 5 and 60, implying that throughout the year pollinators were much more abundant than nectar robbers and that the probability of a flower to be pollinated is always higher than that of being robbed.

Keywords: Multiple ecological interactions, hummingbirds, pollination, nectar robbers, *Diglossa baritula*, Western Mexico, tropical montane forest.

Resumen

Los ladrones de néctar son animales que extraen el néctar producido por las plantas como recompensa para sus polinizadores legítimos sin tener contacto con las partes reproductivas de las flores. El efecto de los ladrones de néctar, ya sea negativo, neutral o positivo, depende en parte de las abundancias relativas de ladrones y polinizadores, ya que esto influencía las probabilidades de daño a las flores en relación con las de polinización, así como la probabilidad de encuentros agonísticos polinizador-ladrón. El propósito de este estudio es proveer una descripción general de la dinámica temporal (a lo largo de un año) y espacial (en dos zonas de vegetación contrastante) en i) la disponibilidad de flores ii) en el uso que de estos recursos hacen polinizadores y iii) ladrones, asi como en los números relativos de polinizadores y ladrones de néctar, como un primer paso para entender el papel de los ladrones de néctar en los sistemas mutualistas plantas-colibríes.

La comunidad consiste de 17 especies de colibríes, 2 ladrones de néctar y 21 especies de plantas visitadas por aves nectarívoras. Las abundancias de aves y plantas muestran dos picos, uno en el invierno y el otro en la época de lluvias. Los colibríes presentan variaciones altas a lo largo del año tanto en el número de individuos como en el número de especies presentes. Solo ocho especies de colibríes y el ladrón de néctar _Diglossa baritula_ se encontraron en las dos áreas, siendo la mayoría mucho más numerosas en las áreas quemadas en donde se capturaron las

demás especies de colibríes. Sin embargo, no se encontraron diferencias estadísticamente significativas entre el número de flores de ambos sitios a lo largo del año. Entre los polinizadores, se encontró una baja especificidad en términos de las especies de plantas visitadas, existiendo algunas especies que son proporcionalmente más usadas que lo que se esperaría de acuerdo a su abundancia. Los colibríes comparten entre sí a muchas de las especies visitadas, al igual que con el ladrón de néctar *D. baritula*. Las plantas son también generalistas en el uso de los polinizadores.

El robo de néctar es un fenómeno muy difundido en el sistema, prevaleciendo en la mayoría de las plantas polinizadas por colibríes en Manantlán. La relación colibríes/ladrones de néctar oscila entre 5 y 60 a lo largo del año, lo que implica que los polinizadores son siempre más abundantes que los ladrones haciendo que la probabilidad de que una flor sea polinizada sea mucho menor a que sea robada.
mayor

INTRODUCTION

Biotic pollination has been customarily regarded as an interaction played (and regulated) by only two partners, the plants and their pollinators (Faegri and van der Pijl 1979). Other factors that may affect the interaction are generally ignored, treating pollination systems as effectively isolated from the rest of the environment. However, microclimatic physical factors such as temperature and humidity affect the quantity and quality of nectar secreted by plants (e.g. Búrquez 1988) which, in turn, may influence the behavior of pollinators and potentially reduce pollen transfer and seed set (e.g. Búrquez 1988, Corbet et al. 1979). The biotic environment on the other hand affects the pollination process. For example, animals that take the floral nectar without contacting the plant's reproductive parts (called nectar robbers, after Inouye 1983) could reduce plant fitness by depleting nectar, damaging reproductive parts and by driving pollinators away (McDade and Kinsman 1980). Nectar robbers can be direct competitors by excluding pollinators from flowers or depleting nectar and thus increasing the time a pollinator must forage to accomplish its metabolic balance (Roubick 1982). On the other hand, by depleting nectar from flowers, 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 their shaking movements during piercing lead to the transference of pollen (Hawkins 1961) or when accidentally become dusted with pollen which is then transported to the next flower to be pierced (Graves 1982, Koeman-Kwak 1973, Macior 1966). Nectar robbers can also be commensals of both plants and pollinators if i) nectar is not a limiting factor for pollinators and nectar availability on the plant 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. For pollinators, if nectar is not a limiting factor, the presence of the robbers may also be of neutral effect (Inouye 1983).

The effect of robbers upon pollination systems depends not only on their direct effect on individual flowers, but also on the abundance and relative frequency of pollinators, robbers and plants (flowers), and in the way these fluctuate through time (Soberón and Martínez del Río 1985). In this context, if pollinators are always more abundant than robbers, the frequency of damaged flowers will be small compared to those pollinated and, the frequency of encounters between pollinators and robbers will also be small. Under these conditions, the impact of robbers upon pollination systems might be small. Thus, to 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) and also in terms of the extent of nectar use by pollinators and robbers. Resource availability (nectar) in relation to the bird's requirements must also be assessed, as resource shortage could trigger agonistic interactions between the birds that may ultimately lead to either competitive exclusion or coexistence via differential abundance through time or in space.

Tropical montane forests of western Mexico, which have complex systems of hummingbirds, their food-plants and nectar robbers (Ornelas and Arizmendi, in press) represent an appropriate study system for multiple interactions. The purpose of this study is to provide a general description of the temporal dynamics of flower availability and their use by hummingbirds (pollinators) and nectar robbers. This is a necessary step to evaluate the role of nectar robbers on the plant-hummingbird pollination system. In this paper, I describe the variation, within a year in the availability of flowers of hummingbird-pollinated plants, pollinators and nectar robbers. Derived from this, I assess i) the temporal differences in the use of flowers by birds in order to determine if some plant species are used more than predicted by their abundance, and ii) the overlap in resource use by pollinators and robbers throughout a year to search for similarities and differences in the feeding activity of hummingbirds, and among these and nectar robbers and iii) I also analyze the overlap among plants in the use of pollinator services throughout the year to assess possible specificity among plants.

METHODS

Study area

Field work was conducted at the "Laboratorio Natural Las Joyas" (LNLJ), in the mountain range of the Sierra de Manantlán. This reserve is located between the Mexican States of Jalisco and Colima, about 50 km E from the Pacific Coast, in western Mexico (19° 35' N; 104° 16' W). The LNLJ, a preserve owned by the Universidad de Guadalajara, comprises 1245 ha and is situated at 1952 m a.s.l. Mean annual precipitation is 1609 mm (mean of five years) with most of the rain falling between June and October. Mean annual temperature is 14.6° C with very few or no days with temperatures below the freezing point. The vegetation is a mosaic of humid coniferous forest, pine-oak forest, patches of cloud forest located at ravines, and secondary vegetation derived either from burning original forest or from abandoned agricultural areas. A detailed analysis of the structure and composition of the vegetation is given by Guzmán (1985), Saldaña-Acosta and Jardel (1991) and Vázquez **et al.** (1990).

Field procedures

The variation in abundance of hummingbirds, hummingbird-pollinated flowers per plant species and nectar robbers was assessed during monthly visits (8-10 days) to the area from November 1990 to October 1991.

Flower availability

Plants in bloom were monitored to determine which species were visited by robbers and/or hummingbirds and to determine how this varies through the year. These observations were carried out during the first and second days (early morning; half an hour after sunrise) on each monthly visit by an observer that stood in front of one individual plant or patch of each of the blooming plant species (at a distance of between 1 and 4 m). The observer focused on an area that never exceeded 3.5 m in diameter of each blooming plant species, and observations continued until a visit occurred. A flower was recorded as visited by a nectar robber only when the visit was followed by piercing and nectar drinking. In the case of hummingbirds, a visit was defined as an instance in which a bird probed at least one flower, drinking nectar from it. Observations lasted up to 2 hours. If a visit did not occur within 2 hours, the observation was ended. In all cases the species of the visitor was recorded.

I used two individuals or patches of each plant species in bloom (each month) and I chose the individuals in which flowers were present in abundance (at least 50) and for which visibility was appropriate (no vegetation covering the plant). All species in bloom at each month were included in the surveys.

To complement the observations of visits during the monthly censuses of flower availability (see below), the presence of holes produced by nectar robbers flowers was 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. Holes made by Diglossa baritula, the main avian nectar robber at our study site (see below), were easily identified because opposite to the hole remains a puncture resulting from the insertion of the upper mandible, which is used as a hook to maintain the flower stable while piercing with the lower mandible (Colwell 1973, Skutch 1954).

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 x 10 m wide). The transects were located within two contrasting vegetation types: forested and regrowth after fire. The two vegetation areas were chosen as representatives of the study area (i.e. representing the composition of about 90% of the zone; Saldaña-Acosta and Jardel 1991). On each vegetation type, two transects were located by means of a randomly selected number which in turn defined the number of meters from the beginning of a trail where transects were located. Two of them were established in the forested area, which comprises pine humid forest and pine forest-cloud forest transition (hereafter called forested area). The other two were located on a patch of burned regrowth vegetation (burned about 15 years ago; hereafter referred to as non forested area). During flower censuses, for each blooming species detected either by direct observations or suspected by its floral syndrome (as defined by Faegri and van der Pijl 1979) as being visited by hummingbirds, I recorded the number of flowers per individual (or per patch in cases where it was impossible to distinguish individuals), and the number of inflorescences and flowers per inflorescence when appropriate. Plant specimens were collected for further identification in the National Herbarium of Mexico (MEXU). To test for differences in flower abundance between and within the two areas censused, an ANOVA for repeated measures was performed using PROC GLM in SAS (SAS 1987) with the log-transformed data (log $\underline{X}$+1). Transects within an area were used as site replicates for this analysis.

Bird Sampling

Monthly variations of the abundance of nectarivorous birds were assessed by placing 8 mist nets (12 m x 3 m), for 8 hours (beginning at dawn), in two consecutive days in each of the two vegetation areas used for flower availability censuses (forested and non forested). Nets were placed 100 m apart on each transect beginning in the same point as the vegetation transects.

Each bird caught was marked using numbered individual bands. Abundances per species (number of individuals caught per 576 m^2, i.e. 3 X 12 m net X 8 nets X 2 days) were calculated per month per transect, disregarding all repeated captures of the same individuals.

Flower-use by pollinators

Occurrence of 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 fuchsine-stained gel following Beattie (1971). Pollen identifications were made by only one observer (M.C. Arizmendi). My identifications can be considered as reliable given that in a separate test in which 210 randomly chosen preparations, for which the identity of the species was not known to me, I was able to tell the correct identification in 98% of the cases.

The number of individuals of each hummingbird species in which the pollen of a particular species appeared, was used to describe patterns of plant use by hummingbirds, for each sampled month. Expected numbers of plant use as a function of flower abundance were calculated by multiplying the total number of hummingbirds caught in a given month by the proportional abundance of flowers of each plant species in that month. Expected and observed frequencies were contrasted with a *G* test for each month. A correction similar to Bonferroni's test, used in ANOVA procedures, was used setting the significance level at 0.0041 (i.e. 0.05 divided by the number of *G* tests performed).

Overlap in the use of flowers by birds and in the use of pollinators by plants

Similarity in the use of resources (pollinators in the case of plants; flowers in the case of birds) was assessed using the similarity index of Sorensen (Poole 1974). Similarity in the use of plants by the different bird species was assessed grouping birds according to their migratory status: residents (including altitudinal migrants); summer visitors and winter visitors. For plants, similarity matrices were calculated separately for the rainy season (from June to October) and the dry season (from November to May).

RESULTS

I. 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 is shown in Table 2.1. The number of hummingbird-visited species per month ranged from 3 (July) to 12 (September). Flower production varied considerably through the year and there were two blooming peaks, the first during the dry season, from December till March, with 2750 to 22379 total flowers per month and 8 to 10 species in bloom; the second peak occurred in the late wet season, in September, with 21384 flowers and 12 species in bloom (Table 2.1).

There was considerable variation in the number of flowers per transect both within each area and between areas all through the year (Fig. 2.1A). The number of flowers per transect was statistically indistinguishable between the two censused areas

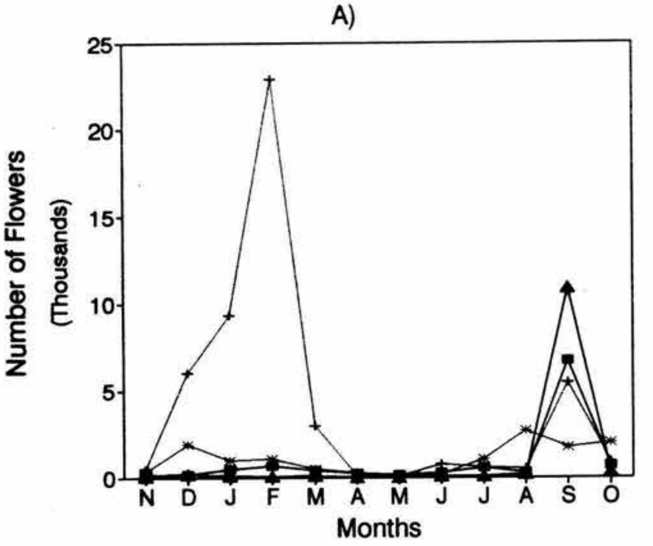
Table 2.1. Plant species and the number of flowers (per 6000m²) (or inflorescences in Calliandra grandifolia and Cirsium jaliscoense) of the plants visited by nectarivorous birds at Sierra de Manantlán, Jalisco. Data correspond to months of 1990 (N-D) and 1991 (J-O).

Species	N	D	J	F	M	A	M	J	J	A	S	O
Bomarea hirtella	0	0	0	0	0	0	0	0	0	196	174	0
Byttneria catalpifolia	0	0	0	0	0	0	0	0	247	1278	714	8
Calliandra grandifolia	103	108	0	0	0	0	0	0	0	0	0	18
Castilleja	-	*	*	*	-	-	-	-	-	-	-	-
Cestrum	52	0	0	0	0	0	0	0	0	24	214	0
Cirsium jaliscoana	0	0	0	8	12	18	2	0	0	0	0	0
Crusea coccinea	0	0	0	0	0	0	0	0	59	276	16991	126
Fuchsia microphylla	376	1206	572	480	63	48	163	1072	1702	1207	1750	2402
Fuchsia fulgens	0	0	0	0	0	3	2	2	19	15	10	0
Ipomoea heredifolia	0	41	8	15	35	12	1	0	5	0	6	11
Ipomoea orizabaensis	7	244	425	318	8	0	0	0	0	0	0	0
Lobelia laxiflora	5	71	173	434	746	467	65	0	23	0	7	0
Malvaviscus arboreus	26	23	11	17	4	0	0	0	11	82	39	240
Moussonia elegans	0	71	209	126	0	0	0	0	0	0	0	0
Phaseolus coccineus	136	0	0	0	0	0	0	0	0	0	570	562
Psittacanthus ramiflorus	*	-	-	-	-	-	*	*	*	*	*	*
Salvia mexicana	205	826	466	460	442	36	5	0	0	0	0	0
Salvia lavanduloides	0	0	0	0	0	0	0	0	0	15	9	78

Table 2.1 Continued.....

Salvia iodantha	24	161	8008	20130	2275	34	0	0	0	0	0	0
Stachys aff. liundenii	0	0	0	0	0	0	7	0	8	192	181	39
Tillandsia	-	-	*	*	-	-	-	-	-	-	-	-
Species	10	9	9	10	8	6	7	3	9	10	12	9
Flowers per month	925	2751	9872	22379	3585	618	245	1074	2074	3285	21384	3486

* plants in bloom, but not counted in the censuses;- same plants not in bloom.



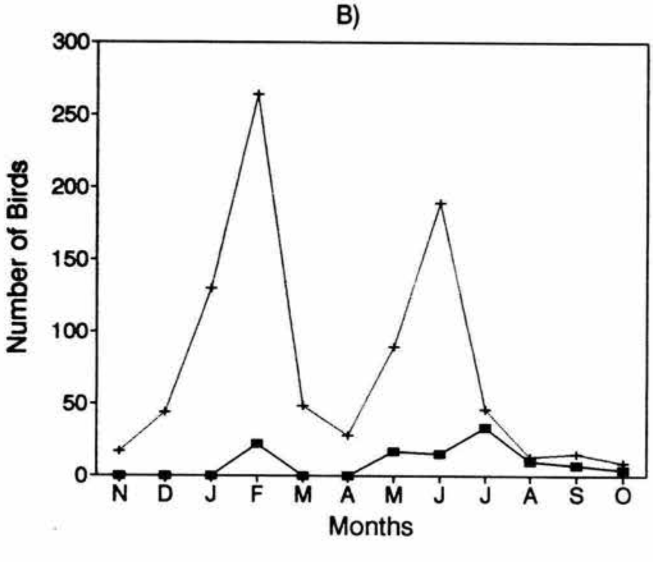


FIGURE 2.1. Abundance of flowers visited by hummingbirds and nectarivorous birds in the two areas censused (A), and number of captured nectarivorous birds in the two areas censused (B). Forested area: solid line; ■=transect 1, ▲=transect 2; non forested area: dotted line; +=transect 1, *=transect 2.

(Repeated measures ANOVA, $\underline{F}_{(1,2)}=1.2$, $\underline{P} > 0.38$).

In the dry season (December to February) the non-forested area showed a marked increase in the number of flowers, due almost completely to the blooming of Salvia iodantha (cf. Table 2.1). 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. 2.1A) with Crusea coccinea contributing with 51% of the total number of flowers produced in the non-forested area and 93.8% in the forested area.

Eleven out of 21 plant species (52.4%) visited by nectarivorous birds (Table 2.2) 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 were tubular. The twenty one species of visited plants bore flowers whose color was close to red with a predominance of red (35%) and orange (30%).

II. The Birds

Seventeen species of hummingbirds and two of nectarivorous passerine birds were caught during the year of netting (Table 2.3). There was a range of 5 to 13 species per month, with February showing the maximum numbers 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; two species which spent more than half of the year in the area and migrate altitudinally; and

Table 2.2. Plant life form and morphological features of flowers visited by hummingbirds and nectar robbers at Sierra de Manantlán, Jal.

Species	Biological Form	Flower Shape	Color	Arrangement	Pol.
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 jaliscoana	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

* Pol.= Pollinator: H= Hummingbird; I= Insect; PB= Perching bird.

five summer visitors which were also altitudinal migrants but stayed in the area less than three months (Table 2.3). Two nectar-robbers were detected: one resident, (Diglossa baritula), and one winter visitor (Vermivora ruficapilla) which was caught only in February (Table 2.3). The winter visitors stayed in the area for periods ranging from one month, February (3 species) or January (1 species), to the whole winter season (3 species). With the exception of Phaethornis superciliosus which stayed in the area for about 3 months, the summer visitors remained only for one month. The altitudinal migrants stayed in the area from winter to early summer.

The abundance of nectarivorous birds changed considerably through 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 transects 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). There were significant differences in the relative abundance of hummingbirds between transects (log-linear model $X^2 = 86010$; $DF = 3$; $P < 0.005$). There were two marked peaks of abundance during the year in the non-forested transects (Fig. 2.1B). In the forested area, numbers were small throughout the year, showing an increase in the rainy season, from June to September. In the non-forested area numbers remained comparatively high throughout the year, but there were abrupt increases in February and June. The first peak was explained by the massive arrival of long-distance migrants and the second was due to the arrival of the altitudinal vagrants

Table 2.3. Number and residence status of nectarivorous birds captured in a 576 m² netting area per month in two sites at Sierra de Manantlán,Jal.

Species	N	D	J	F	M	A	M	J	J	A	S	O
ALTITUDINAL MIGRANTS												
Amazilia beryllina	0	3	21	81	21	2	14	72	0	0	0	0
Colibri thalassinus	1	3	18	15	1	1	1	2	0	0	0	0
RESIDENTS												
Atthis heloisa	1	3	3	17	2	4	3	2	1	1	1	1
*Diglossa*** *baritula*	1	2	14	9	4	5	12	5	11	2	1	1
Eugenes fulgens	0	0	3	9	0	0	3	2	1	1	2	2
Hylocharis leucotis	7	5	20	29	7	10	61	92	19	1	3	1
Lampornis amethysthinus	3	1	2	21	1	6	10	21	44	18	15	3
SUMMER VISITORS												
Amazilia rutila	0	0	0	0	0	0	0	2	0	0	0	0
Calothorax lucifer	0	0	0	0	0	0	0	1	0	0	0	0
Cynanthus latirostris	0	0	0	0	0	0	0	1	0	0	0	0
Phaethornis superciliosus	0	0	0	0	0	0	2	2	2	0	0	0
WINTER VISITORS												
Archilochus alexandrii	0	1	0	0	0	0	0	0	0	0	0	0
Amazilia violiceps	0	0	0	1	0	0	0	0	0	0	0	0
Stellula calliope	0	1	2	1	1	0	0	0	0	0	0	0
Selasphorus platycercus	2	7	11	7	3	0	0	0	0	0	0	2
Selasphorus rufus	2	19	35	24	8	0	0	0	0	0	0	0
Selasphorus sassin	**s**	**s**	**s**	**s**	**s**	0	0	0	0	0	0	0
Tilmatura dupontii	0	0	0	3	0	0	0	2	0	0	0	0
Vermivora ** *ruficapilla*	0	0	0	71	0	0	0	0	0	0	0	0
Species	7	10 9	10 11	13	9	6	8	12 11	6	5	5	6.
Birds per month	17	44	130	288	48	28	106	204	79	23	22	13

** nectar robbers; **s**= sighted but not captured.
that visited the area for a short time.

Eight out of 17 species of hummingbirds plus the robber *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*, *S. sassin* and *Tilmatura dupontii*) and the robber *V. ruficapilla* were found only in the non-forested area. Nine species were recorded in both areas (Table 2.4), and a test performed to look for differences in habitat use indicated that all nectarivorous bird species were considerably more abundant in the non-forested area (overall comparison X^2 466.12, $P < 0.001$). Individual tests with Yates' correction (Zar 1984) for each species and taking significance level as 0.005 (because of the use of repeated tests ie, 0.05/9, as used in Bonferroni corrections for t test, Zar 1984) showed that all species, except *P. superciliosus* ($X^2 = 1.5$, $DF = 1$; $P > 0.1$) and *Lampornis amethysthinus* ($X^2 = 7.06$, $DF = 1$; $P > 0.005$), were statistically more abundant in the nonforested area (X^2 for *Amazilia beryllina* 185.5, *Atthis heloisa* 29.64, *Colibri thalassinus* 32.59, *D. baritula* 28.48, *Eugenes fulgens* 12.04, *Hylocharis leucotis* 173.91, *Selasphorus platycercus* 12.97; $DF = 1$; $P < 0.005$ in all cases).

The ratio hummingbird/robber abundance showed that all through the year pollinators were more abundant than robbers (Fig. 2.2), with a value of 5 (April) to 60 (June) times more pollinators than robbers.

III. Patterns of interaction between plants and birds

Some plant species were visited during almost throughout their bloom, or at least in their blooming peak by many species of pollinators (Table 2.5). *Hylocharis leucotis* and *L. amethysinus*

Table 2.4. Comparison of the abundances of the hummingbird species common to forested and nonforested sites in Manantlán, Jalisco.Data are cumulative numbers of individuals captured in each zone in all the year. Expected values (in parenthesis) were derived assuming equal partition of the total number of birds in the two sites.

Hummingbird Species	FOREST	NON FOREST
Amazilia beryllina	7 (107)	207 (107)
Atthis heloisa	2 (19.5)	37 (19.5)
Colibri thalassinus	2 (21)	40 (21)
Diglossa baritula	11 (34)	56 (34)
Eugenes fulgens	3 (12)	21 (12)
Hylocharis leucotis	22 (128)	234 (128)
Lampornis amethystinus	56 (72.5)	89 (72.5)
Phaethornis superciliosus	1 (3)	5 (3)
Selasphorus platycercus	6 (17)	28 (17)

$X^2 = 466.12$; $DF = 8$; $P < 0.001$

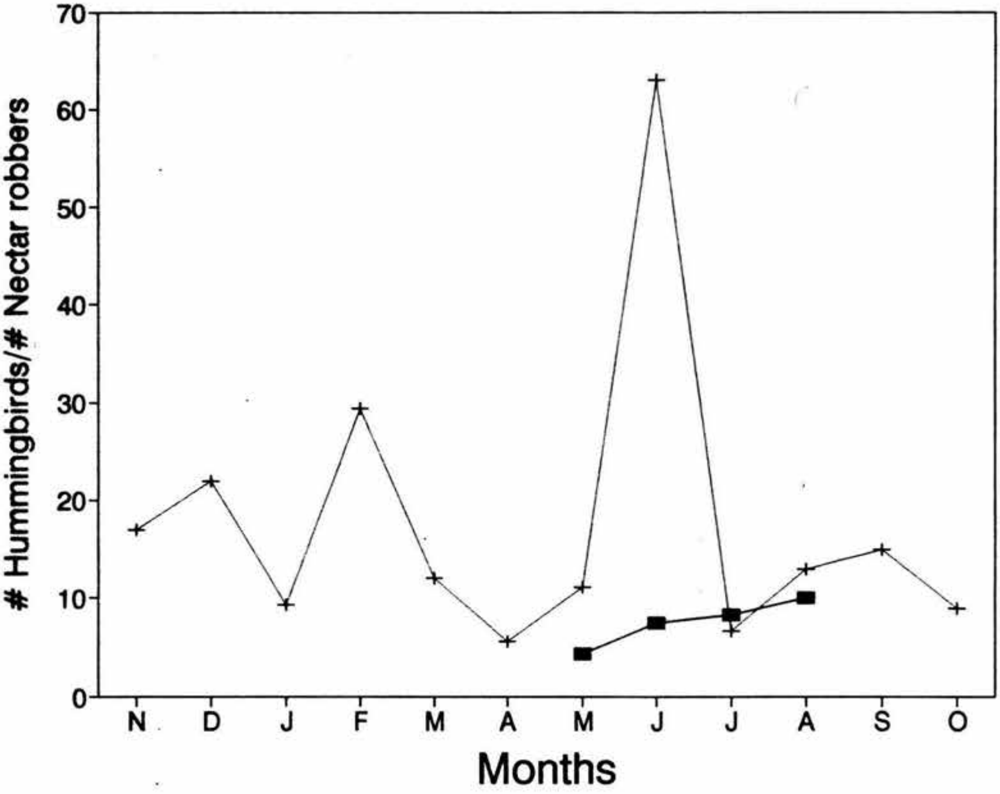


FIGURE 2.2. Time course of the ratio pollinators/nectar robbers in the two zones sampled (Forested, ■;Non Forested, +) in Manantlán, Jalisco.

Table 2.5. Number of species of hummingbirds that visited flowers of each of the plant species in all months of the sampled year.

Species	N	D	J	F	M	A	M	J	J	A	S	O
Bomarea hyrtella	-	-	-	-	-	-	-	-	-	2	2	2
Byttneria catalpifolia	-	-	-	-	-	-	-	-	2	1	1	1
Calliandra grandifolia	1	4	-	-	-	-	-	-	-	-	-	1
Castilleja sp.	-	1	1	1	-	-	-	-	-	-	-	-
Cestrum sp.	1	-	-	-	-	-	-	-	-	-	1	1
Cirsium jaliscoense	-	-	-	4	3	3	3	-	-	-	-	-
Crusea coccinea	-	-	-	-	-	-	-	-	2	1	1	1
Fuchsia fulgens	-	-	-	-	-	2	2	2	3	2	3	-
Fuchsia microphylla	2	4	6	3	1	3	3	3	4	2	4	3
Ipomoea heredifolia	-	2	4	4	2	3	2	2	-	-	1	1
Ipomoea orizabaensis	2	2	2	2	2	-	-	-	-	-	-	-
Lobelia laxiflora	1	2	3	6	7	5	6	-	1	-	4	-
Malvaviscus arboreus	1	1	1	1	2	-	-	-	2	1	1	1
Mousonia elegans	-	2	2	1	-	-	-	-	-	-	-	-
Phaseolus coccineus	4	-	-	-	-	-	-	-	-	-	4	3
Psittacanthus ramiflorus	*2*	-	-	-	-	-	*5*	*5*	*2*	*2*	*1*	*3*
Salvia iodantha	5	8	8	10	7	5	-	-	-	-	-	-
Salvia lavanduloides	-	-	-	-	-	-	-	-	-	4	4	8
Salvia mexicana	5	8	8	10	7	5	1	-	-	-	-	1
Tillandsia sp.	-	-	2	2	-	-	-	-	-	-	-	-
Stachys aff.liundenii	-	-	-	-	-	-	5	-	-	1	1	3

were the most common visitors for all the plants all year round. The only seemingly specialized plant appears to be the long-tubed Fuchsia fulgens, visited only by the two larger hummingbirds (P. superciliosus and E. fulgens) and occasionally by the vagrant A. rutila. Phaethornis superciliosus was also the only hummingbird that could be considered specialized in visiting only this plant species, when it was in full bloom, using flowers of Psittacanthus ramiflorus and Lobelia laxiflora when it arrived to the area. Accordingly, its abundance closely followed that of F. fulgens flowers.

Flower-use by pollinators and robbers

An interaction matrix showing the proportion of hummingbirds of each species in which pollen of a given plant species was found is presented in Table 2.6. 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 and analyzed in all the blooming season of each plant species. In all cases pollen loads were mixed. The interaction matrix shows that while pollen of some plant species (e.g. Malvaviscus arboreus) was present in only a few hummingbirds of a few species, others (e.g. Salvia mexicana and S. iodantha) were present in many birds of many species. Many other situations occurred in between these two extremes. Likewise, 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 plants species; again there were many situations in between. This matrix suggests that hummingbirds used some plants more than others. This tendency was tested against the hypothesis that birds used flowers according only to their relative flower abundance in each

Table 2.6. Proportion of hummingbirds that bore polen of a given plant species.
For nectar-robbers (Db and Vr) only visited (*) and Non-visited plants (-) are indicated.

							Species (number) of birds								
Plant Species	Ab (205)	Ah (38)	Ar (2)	Av (1)	Ct (40)	Ef (24)	Hl (256)	La (145)	Ps (6)	Sp (28)	Sr (88)	Sc (5)	Td (5)	Db	Vr
Bomarea hirtella	x	1.00	x	x	1.00	0.00	1.00	0.18	0.50	x	x	x	x	*	-
Byttneria catalpifolia	x	0.00	x	x	x	0.00	0.03	0.17	x	0.00	x	x	x	*	-
Calliandra grandiflora	0.33	0.00	x	x	0.50	1.00	0.36	0.71	x	0.27	0.10	0.00	x	*	-
Cestrum sp.	0.00	x	x	x	0.00	0.40	0.08	0.00	x	1.00	0.50	x	x	*	-
Cirsium jaliscoense	0.05	0.04	0.50	1.00	0.00	0.08	0.02	0.03	0.00	0.17	0.00	0.00	0.00	*	-
Crusea coccinea	0.01	0.00	1.00	x	1.00	0.15	0.31	0.20	0.00	1.00	x	x	x	-	-
Fuchsia microphyla	0.04	0.05	0.50	0.00	0.04	0.33	0.18	0.34	0.00	0.18	0.06	0.00	0.20	*	-
Fuchsia fulgens	0.00	0.00	0.50	0.00	0.00	0.88	0.00	0.24	0.50	1.00	x	x	x	*	-
Ipomoea heredifolia	0.06	0.05	0.00	0.00	0.02	0.17	0.04	0.10	0.00	0.04	0.05	0.00	0.00	*	-
Ipomoea orizabaensis	0.01	0.00	x	0.00	0.00	0.33	0.00	0.00	x	0.00	0.00	0.00	0.00	*	-
Lobelia laxiflora	0.22	0.21	1.00	x	0.18	0.29	0.45	0.12	0.17	0.32	0.08	0.20	0.00	*	-
Malvaviscus arboreus	0.00	0.00	x	0.00	0.00	0.06	0.00	0.03	0.00	0.04	0.00	0.00	0.00	*	-
Phaseolus coccineus	0.67	0.67	x	x	1.00	1.00	1.00	1.00	x	0.18	0.14	x	x	*	-
Psittacanthus ramiflorus	0.18	0.44	1.00	x	0.75	0.58	0.34	0.39	0.17	0.75	1.00	x	0.00	*	-
Salvia lavanduloides	x	1.00	x	x	1.00	0.00	0.75	0.03	x	1.00	x	x	x	-	-
Salvia mexicana	0.74	0.62	1.00	1.00	0.95	0.40	0.51	0.30	x	0.96	0.73	0.80	0.60	*	*
Salvia iodantha	0.73	0.62	1.00	1.00	0.95	0.40	0.48	0.30	x	0.92	0.73	0.80	0.60	*	*
Stachys aff.liundenii	0.25	0.00	1.00	x	x	0.13	0.01	0.11	0.50	1.00	x	x	x	-	-
Tillandsia sp.	0.05	0.05	x	0.00	0.16	0.09	0.10	0.00	x	0.14	0.08	0.33	0.00	*	-

Abbreviations for nectarivorous birds (Columns): Ab, Amazilia beryllina;
Ah, Atthis heloisa; Ar, Amazilia rutila; Av, A.violiceps
Ct, Colibri thalassinus; Ef, Eugenes fulgens; Hl, Hylocharis leucotis;
La, Lampornis amethystinus; Ps, Phaethornis superciliosus;
Sp, Selasphorus platycercus; Sr, S.rufus; Sc, Stellula calliope;
Td, Tilmatura dupontii; Db, Diglossa baritula; Vr, Vermivora ruficapilla.
x indicates that species of plant and bird do not coincide temporaly.

month. This hypothesis was rejected, overall, showing that the guild of hummingbirds used some species more than others (Table 2.7; Appendix 2.1). However, there was considerably variation in the use of the different plant species by hummingbirds throughout the year. In December S. iodantha and S. mexicana were used more than predicted. The same situation prevailed all through their blooming period for S. mexicana, but S. iodonatha was used less than expected in January, February and March (Appendix 2.1). Other species that were also used more than expected were Ipomoea heredifolia, Cirsium jaliscoense, and F. fulgens. On the other hand, Fuchsia microphylla was used according to its flower abundance or less than expected in January, and from April to June. Lobelia laxiflora was sometimes used as expected, sometimes preferred and sometimes underused. Plant species used less than expected according to their abundance include F. microphylla, Byttneria catalpifolia and Phaseolus coccineus in some months.

With regards to the robbers, it was found that D. baritula robs by making a little hole in the basis of the corolla using its upper mandible as a hook that maintained immobile the flower and with its inferior mandible pierced the corolla, while V. ruficapilla robs by cutting the entire corolla and sucking nectar through the back of the severed corolla, and throwing away the entire corolla afterwards. Diglossa baritula visited all hummingbird flowers except for C. coccinea, Stachys aff. liundenii and Salvia lavanduloides, all of them small herbs. For most of the year D. baritula visited more than 85% of the plant species pollinated by hummingbirds (Fig. 2.3).

Additionally, I found pollen of P. ramiflorus, C. jaliscoense, B. catalpifolia and Calliandra grandifolia on D.

Table 2.7. Results of an evaluation (G test) of differential use of the plant species visited by the hummingbirds each month at Sierra de Manantlán, Jalisco. Full data set in Appendix 2.1.

Month	G	df
November	45.62 **	6
December	270.91 **	7
January	265.09 **	5
February	375.65 **	6
March	58.64 **	5
April	163.57 **	5
May	206.60 **	6
June	357.41 **	3
July	60.49 **	6
August	83.83 **	5
September	292.89 **	9
October	88.89 **	7

Significance level taken as 0.0041 (Bonferroni corrections for repeated tests; 0.05/12) **.

baritula's head. Vermivora ruficapilla was observed robbing flowers of S. mexicana and S. iodantha.

Overlap in the use of flowers by birds and of pollinators by plants

Hummingbirds in general shared among them many plant species as indicated by the high values of Sorensen's similarity indices of the use of plant species (Table 2.8). The overlap in the use of resources was higher among residents (0.7-0.9; mean= 0.81) than in winter (0.2-0.8; mean= 0.52) and summer (0-0.5; mean= 0.33) visitors. Diglossa baritula was very similar in the use of resources to all the resident hummingbirds (means range between 0.7 and 0.9). From the plant's perspective, similarity indices of the hummingbirds acting as pollinators were considerably high in general. Indices ranged from 0.3 to 0.9 (mean= 0.62) in the wet season and from 0.4 to 1.0 (mean= 0.73) in the dry season. The only cases of relative specialization are P. superciliosus and E. fulgens among hummingbirds, and F. fulgens among plants, as described above.

DISCUSSION

The results of this study showed that Manantlán holds a very high diversity of hummingbirds, with almost 30% of the Mexican hummingbird fauna. This makes this hummingbird community one of the two more diverse so far documented, with species richness second only to that reported by Stiles (1980) for a tropical wet forest in Costa Rica, nine degrees of latitude nearer the equator. If compared with other sites of similar elevation studied (e.g. Brown and Kodric-Brown 1979, Wolf et al. 1976) this locality's species richness appears to be special, having more

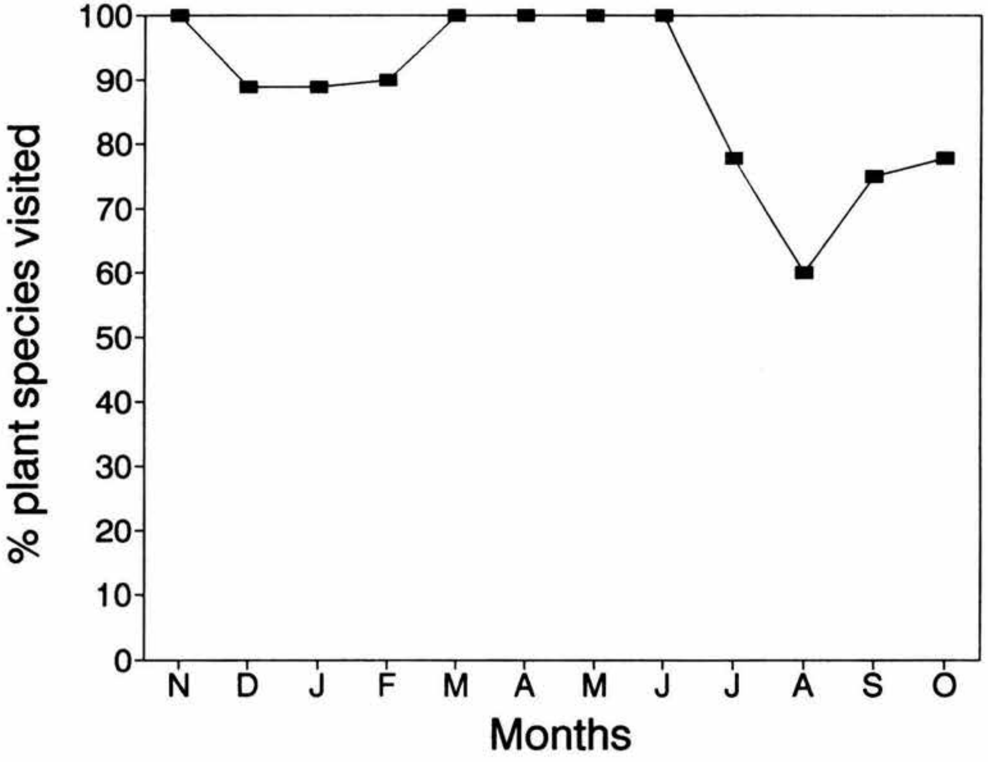


FIGURE 2.3. Time course of the percentage of plant species visited (from the total hummingbird-visited plants) by Diglossa baritula in Manantlán, Jalisco.

Table 2.8. Sorensen's similarity index for comparison of the use of flowers by birds (Part I) and for the use of pollinators by flowers (Part II) in Manantlán, Jalisco.

I: Birds

a) Residents

	La	Hl	Ah	Ef	Ab	Ct	Db
La		0.9	0.7	0.8	0.8	0.8	0.9
Hl			0.9	0.8	0.9	0.9	0.8
Ah				0.7	0.8	0.9	0.7
Ef					0.9	0.7	0.9
Ab						0.8	0.7
Ct							0.7
Db							

b) Winter visitors

	Sr	Sp	Sc	Av	Vr
Sr		0.8	0.6	0.3	0.3
Sp			0.5	0.3	0.2
Sc				0.8	0.6
Av					0.8
Vr					

c) Summer visitors

	Ps	Td	Ar
Ps		0	0.5
Td			0.4
Ar			

II: Flowers

a) All Year

	Fm	Ih	Ll	Ma
Fm		0.9	0.9	0.5
Ih			0.8	0.5
Ll				0.4
Ma				

b) Wet Season

	Bh	Bc	Ff	Pc	Ce	Cc	Pr	St
Bh		0.4	0.5	0.7	0.5	0.6	0.8	0.6
Bc			0.5	0.4	0.3	0.4	0.3	0.4
Ff				0.6	0.4	0.7	0.7	0.8
Pc					0.8	0.6	0.5	0.6
Ce						0.8	0.9	0.8
Cc							0.8	0.9
Pr								0.8
St								

c) Dry Season

	Cg	Cj	Io	Sl	Sm	Si	Tsp
Cg		0.6	0.4	0.8	0.8	0.8	0.8
Cj			0.4	0.6	0.8	0.8	0.6
Io				0.6	0.8	0.8	0.6
Sl					0.9	0.7	0.9
Sm						1	0.8
Si							0.8
Tsp							

Table 2.8 Continued...

Abbreviations for birds: 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, *S. rufus*; Sc, *Stellula calliope*; Td, *Tilmatura dupontii*; Db, *Diglossa baritula*; Vr, *Vermivora ruficapilla*.

Abbreviations for plants: Bh, *Bomarea hirtella*, Bc *B. catalpifolia*, Bc, *B. catalpifolia*; Cg, *C. grandiflora*; Cs, *Cestrum* sp.; Cc, *C. coccinea*;Fm, *F. microphylla*; Ff, *F. fulgens*; Ih, *I. heredifolia*; Io, *I. orizabaensis*; Ll, *L. laxiflora*; Ma, *M. arboreus*; Pc, *P. coccineus*; Pr, *P. ramiflorus*; Sm, *S. mexicana*; Si, *S. iodantha*; Sl, *S. lavanduloides*; St, *S. a. liundenii*; Tsp., *Tillandsia* sp.

than three times the species of hummingbirds reported so far. This might be explained by the fact that in some of the other comparable communities, the studies have been restricted to give a description of the plant-hummingbird interactions in only one season of the year, or have concentrated on some particular plants and their pollinators. The occurrence of such a diverse system for Manantlán stresses the need of using a general and descriptive approach to studying plant-hummingbird interactions to understand the magnitude of the network of interactions occurring in bird pollination systems.

However, in the studied system only two avian nectar robbers were detected, one, V. ruficapilla, a winter visitor that only stayed in the area for a month and the other, D. baritula, was a resident acting as a visitor for many of the plants pollinated by hummingbirds.

The prevalence of nectar robbing in the system is high, with almost all plant species pollinated by hummingbirds in the area being pierced by D. baritula. This study represents the first yearly evaluation of the prevalence of this phenomenon. The results are in agreement with the idea that D. baritula is specialized in piercing hummingbird-pollinated plants (Skutch 1954, Faegri and van der Pijl 1979). This high prevalence can be taken as a measure of the commonness of the phenomenon but also as a first indication of its possible importance, in terms of its possible effect upon the mutualistic system.

Seasonal variation in the use of plant species was found to be similar between hummingbirds and D. baritula. The temporal use of plants by D. baritula followed a similar pattern to that of the resident hummingbirds. Moreover, the robber and the hummingbirds used plants with flowers of particular morphological characteristics (tubular or cup-shaped and red or orange in color). This stresses both i) its specialization and its "hummingbird-like" behavior that was first recognized in 1871 (Vallada op. cit.) and accepted until now (see Faegri and van der Pijl 1979), and ii) its argued convergence in morphological traits such as the tongue and bill shapes (Vuilleumier 1969).

Given the high overlap in 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 effect depends on the ratio pollinators/ robbers, both for the plants and for pollinators (Soberón and Martínez del Río 1985). The results of this work show that throughout the year hummingbirds were always more abundant than robbers, being their numbers between 5 and 60 times higher. This implies that 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 be also slow.

Nectar robbers can be regarded as pollinators of some plants (Inouye 1983). In this study I documented the presence of pollen of four plant species in the robber's body. It is possible that at least for these four species _D. baritula_ might act as a pollinator. These four species can be grouped according to their pollination syndrome (Faegri and van der Pijl 1979) in two classes 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), which keep the nectar concealed in the bottom of the tube.

Pollination in the latter could take place as a result of dusting the robber's body while piercing. A similar situation is reported for Diglossa sp. and the mistletoe Tristerix longebracteanus in Perú (Graves 1982). In this case the bird is dusted with pollen while trying to pierce internal flowers from an external perch. All of these plants bear their flowers in inflorescences, the clumping of the flowers being one of the possible causes of dusting with pollen, and thus pollination.

Diglossa baritula can be regarded as a specialized nectar-feeding bird and as dependent on the mutualistic system formed by hummingbirds and plants pollinated by them. Its effect upon the mutualistic interaction studied here is apparently slight, due to the high pollinators/robbers ratio throughout the year. Vermivora ruficapilla can be considered as specialized in its short stay, with a role comparable to that of other insectivorous birds that, when wintering, change their diet consuming fruits and nectar.

The high overlap both among birds (both pollinators and robbers) in the use of flowers and between plants in the use of pollinator's services and the spatio-temporal variability in the specific and numeric composition of the visitant's guild makes that the ecological and evolutive consequences for the plant of the presence of nectar robbers are difficult to be drawn as one individual plant can have flowers visited by different pollinators and robbers, and the combination of both, being the plant fitness the sum of the effects upon each individual flower. To understand the role of the nectar robbers in the pollination system, more detailed studies are needed where particular plant species and the guild of visitants can be analyzed. However, the approach used in this paper, at the community level, is necessary as a way to detect the prevalence of the phenomenon and the potentiality of each species to be studied. At this level of approach, the system seems complex and diverse and the effects of the robber on the mutualistic association slight.

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Appendix 2.1. G tests to calculate differential use of the diferent plant species by hummingbirds. Observed values (fi) were number of hummingbirds in which pollen of each plant species appeared. Expected values (Fi) were calculated according to flower proportional abundance in each month (see text for details).

Species	fi	Fi	
November			
Calliandra grandifolia	1	6.4	
Cestrum sp.	1	2	
Fuchsia microphylla	5	16.4	
Lobelia laxiflora	1	0.8	
Phaseolus coccineus	8	5.2	
Salvia mexicana	12	7.2	
Salvia iodantha	12	2	G= 45.624
December			
Bomarea hirtella	3	0.12	
Calliandra grandiflora	7	2.65	
Fuchsia microphylla	11	27.14	
Lobelia laxiflora	2	1.45	
Salvia mexicana	46	16.95	
Salvia lavanduloides	41	98.14	
Salvia iodantha	46	3.31	
Ipomoea heredifolia	2	8.21	G= 270.91
January			
Fuchsia microphylla	8	13.23	
Ipomoea heredifolia	5	0.73	
Ipomoea orizabaensis	2	10.14	
Lobelia laxiflora	3	4.20	
Salvia mexicana	109	18.88	
Salvia iodantha	109	188.88	G= 265.09
February			
Cirsium jaliscoana	8	0.082	
Fuchsia microphylla	5	4.96	
Ipomoea heredifolia	8	1.50	
Ipomoea orizabaensis	1	2.86	

Lobelia laxiflora	22	4.12	
Salvia mexicana	81	10.21	
Salvia iodantha	81	182.24	*G*= 375.65

March

Cirsium jaliscoana	3	0.58	
Fuchsia microphylla	3	2.88	
Ipomoea heredifolia	6	1.88	
Lobelia laxiflora	43	29.15	
Salvia mexicana	45	22.76	
Salvia iodantha	45	87.72	*G*= 58.62

April

Cirsium jaliscoana	3	4.08	
Fuchsia microphylla	6	13.44	
Fuchsia fulgens	3	1.19	
Lobelia laxiflora	39	91.75	
Salvia mexicana	38	8.07	
Salvia iodantha	37	7.44	*G*= 163.57

May

Cirsium jaliscoana	26	0.75	
Fuchsia microphylla	12	55.53	
Ipomoea heredifolia	5	0.37	
Lobelia laxiflora	38	27.93	
Salvia mexicana	8	4.73	
Salvia iodantha	5	5.25	
Fuchsia fulgens	1	0.42	*G*= 206.60

June

Fuchsia microphylla	15	80.41	
Fuchsia fulgens	3	0.23	
Phaseolus coccineus	4	7.25	
Lobelia laxiflora	70	4.10	*G*= 357.41

July

Bittneria catalpifolia	11	7.53	
Crusea coccinea	13	1.95	
Fuchsia microphylla	35	57.96	
Ipomoea heredifolia	8	0.94	

Lobelia laxiflora	1	0.7	
Mousonia elegans	1	0.33	
Stachys aff. liundenii	1	0.57	G= 60.49

August

Bittneria catalpifolia	5	14.52	
Crusea coccinea	6	3.44	
Fuchsia microphylla	14	13.98	
Fuchsia fulgens	11	0.16	
Mousonia elegans	1	3.07	
Stachys aff. liundenii	1	2.80	G= 83.83

September

Bittneria catalpifolia	3	1.77	
Bomarea hirtella	2	0.29	
Cestrum sp.	1	0.41	
Crusea coccinea	3	42.83	
Fuchsia microphylla	10	3.97	
Fuchsia fulgens	9	0.02	
Ipomoea heredifolia	5	0.01	
Lobelia laxiflora	3	0.01	
Phaseolus coccineus	14	1.16	
Stachys aff. liundenii	1	0.49	G= 292.89

October

Bittneria catalpifolia	1	0.44	
Fuchsia microphylla	5	16.93	
Ipomoea heredifolia	2	1.47	
Mousonia elegans	1	1.47	
Phaseolus coccineus	4	4.10	
Salvia lavanduloides	5	0.27	
Stachys aff. liundenii	1	0.25	
Lobelia laxiflora	6	0.04	G= 80.89

Capítulo III

El ladrón de néctar Diglossa baritula: las plantas de las que se alimenta y el efecto sobre los colibríes y las plantas polinizadas por ellos.

Feeding Ecology of the slaty flower-piercer Diglossa baritula (Passeriformes: AVES): Prevalence of nectar robbery and effects on reproduction of hummingbird-pollinated plants in a Mexican highland tropical forest.

Abstract

Birds of the genus Diglossa are known as nectar robbers that pierce corollas of flowers pollinated by hummingbirds. The interaction between hummingbirds, flower-piercers and plants is not well studied and very little is known about the feeding ecology and the natural history of most of the species of Diglossa. This work provides data on the feeding ecology of D. baritula, a bird that inhabits montane forests of southern Mexico and Guatemala. The study was conducted in western Mexico, in the northern-most part of the distribution of the species.

Monthly visits were carried out to record bird numbers, flower availability and visitation patterns, aggressive interactions between robbers and pollinators, and frequency of flowers damaged by the nectar robber.

Diglossa baritula is a resident bird in the area and feeds on 16 plant species, searching primarily for nectar and occasionally (in one plant species) for fruits. During the year of study it had two periods of reproduction, and molting occurred all year round.

Of 16 plants visited by Diglossa baritula 15 were pollinated by hummingbirds and there was only one insect pollinated species which was visited by this robber. Thus flower piercing was a common phenomenon in this community. In all 16 species visited this bird acted as a nectar robber, but in four of them pollen was found on the body of the bird, suggesting it could also act as a pollinator of these plants.

In four plant species studied in detail nearly 50% of all the flowers examined were pierced. However it seems that puncturing does not always damage the flowers. For two plant species examined (*Salvia mexicana* and *S. iodantha*), seed production was not found to be affected by piercing of the corolla.

Only occasionally did territorial hummingbirds fight with *D. baritula*, and when aggressive encounters occurred, hummingbirds did not chase nectar robbers away. *D. baritula* foraged quietly, avoiding attacks from pollinators.

Althought flower piercing by *D. baritula* was a prevalent phenomenon in the community there appears to be a neutral effect on seed production, at least in the two species examined. Its role as the possible pollinator of at least four plant species is also discussed.

Keywords: Slaty flower-piercer, *Diglossa baritula*, nectar robber, hummingbirds, Western Mexico, pollination.

Resumen

Las aves del género Diglossa han sido reconocidas como ladrones de néctar que perforan corolas de flores polinizadas por colibríes. La interacción entre colibríes, plantas y ladrones de néctar del género Diglossa ha sido poco estudiada. El presente trabajo es un análisis de la ecología alimenticia de Diglossa baritula, un ave que habita las montañas del centro y sur de México y Guatemala. Este trabajo se realizó en el límite boreal de la distribución de la especie, en el oeste de Mexico.

Se realizaron visitas mensuales al área de estudio, en donde se registraron las abundancias de colibríes, plantas y del ladrón de néctar, así como algunos parámetros de su interacción como son los encuentros agresivos, y la frecuencia de flores perforadas.

Diglossa baritula es una especie residente en el área que se alimenta del néctar de 16 especies de plantas a lo largo del año, aunque en algunos meses fue observada consumiendo frutos de zarzamora (Rubus sp.). Presentó dos períodos de reproducción, mientras que la muda del plumaje ocurrió a lo largo del año. Visitó plantas principalmente polinizadas por colibríes. En cuatro de las 16 especies de plantas utilizadas por D. baritula se le puede considerar como posible polinizador por haberse encontrado polen de ellas en el cuerpo del animal.

El robo de néctar es un fenómeno común en la comunidad encontrándose que cerca del 50% de las flores examinadas presentaron algún nivel de daño. Por otra parte, los resultados

parecen indicar que la perforación no afecta la producción de semillas en dos especies de plantas (Salvia mexicana y S. iodantha) analizadas.

Se registraron pocos encuentros agresivos entre colibríes y ladrones de néctar. En los que pudieron observarse, se encontró que el colibrí no excluye al ladrón de su territorio. D. baritula visita las flores sin hacer ruido, evitando los ataques de los polinizadores.

El papel de Diglossa baritula como parásito del sistema se discute relacionándolo con la generalidad del fenómeno en el área y la aparente ausencia de efecto sobre la producción de semillas en las dos especies de plantas estudiadas. Se discute además su posible papel como polinizador de cuatro especies de plantas.

INTRODUCTION

Flower-piercing birds (genus Diglossa) include small nine-primaried oscines that feed on nectar, insects, and in some cases fruits. Their more remarkable character is the morphological modification of the bill to feed on nectar (Beecher 1951). Bills have a thin lower mandible of moderate length, slightly upturned and pointed, and a longer upper mandible also upturned, but with a sharp downward hook at the tip (Vuilleumier 1969). Additionally, they have a long brushy and U-shaped tongue to suck nectar from flower nectaries (Moyniham 1963 1968, Skutch 1954). These features allow them to get floral nectar by piercing corollas of, potentially, many kinds of flowers. However, it has been observed that nectar robbery by D. baritula occurs mainly in long, tubular, high-reward flowers (Skutch 1954) such as those pollinated by hummingbirds (Faegri & van der Pijl 1979).

Flowers pollinated by hummingbirds produce nectar in large quantities (Baker & Baker 1975). Nectar secretion consumes a large fraction of the daily produced photosynthate, oscillating between 4.3 and 36.6% in Asclepias syriaca and up to 20% in Medicago sativa (Southwick 1984). Hummingbirds spend and require a lot of energy, resulting from their accelerated metabolism, consuming large amounts of nectar to meet their energetic requirements (Hainsworth & Wolf 1972). For these reasons, it may be assumed that the effect of a robber on the mutualistic system formed by hummingbirds and the plants pollinated by them must be negative due to the high energetic costs of losing nectar for both mutualists. However, the effects of Diglossa upon pollination systems are not well known and it has been regarded sometimes as a parasite of the systems (Lyon & Chadek 1971, Colwell 1973, Colwell **et al.** 1976) and sometimes even as a pollinator (Graves 1982, Martínez del Río & Eguiarte 1987).

In adition to providing information on the natural history of Diglossa baritula, the purpose of this work was to assess the prevalence of nectar robbing by D. baritula and its effect upon a hummingbird pollination system under natural conditions. Specifically, I describe i) the frequency of flower piercing by D. baritula and its variation through a year, ii) the identity, characteristics and flower production of the plants visited by the robber, and iii) its effect upon seed production of some hummingbird-pollinated plants, in a tropical forest of the highlands of western Mexico.

METHODS

Study area.

Field work was conducted at the "Laboratorio Natural Las Joyas" in the mountain range of the Sierra de Manantlán, Jalisco, Mexico (19° 35' N; 104° 16' W) between May 1990 and January 1992. The Laboratorio Natural Las Joyas is a 1245 ha preserve owned by the Universidad de Guadalajara, situated at about 50 km east from the Pacific Coast and at 1952 meters above sea level. Annual mean precipitation is 1609 mm (mean of 5 years) with most of the rain falling between June and October. Mean annual temperature is 14.6° C with very few days a year with temperatures below freezing. The vegetation is a complex mosaic of humid coniferous forest, pine-oak forest, patches of cloud forest located at ravines, and secondary vegetation resulting from either burning or abandoned agricultural areas. A detailed analysis of the structure and composition of the vegetation is given by Vázquez **et al.** (1990), Saldaña-Acosta & Jardel (1991) and Guzmán (1985).

The studied species.

Diglossa baritula is a primary nectar robber because it makes holes by itself (Inouye 1983). This species can also be considered as a competitor of the legitimate pollinators (as they use the same resource) and at the same time as a parasite of the plant (because it removes nectar without contacting the reproductive parts; Soberón & Martínez del Río 1985).

Diglossa baritula occurs in the mountains of Mexico (A.O.U. 1983), with two subspecies (Friedmann **et al.** 1950), D. baritula baritula extending from Jalisco to Veracruz and Oaxaca and D. baritula montana in the southernmost extreme of Chiapas and Guatemala, El Salvador and Honduras. It is a nectarivorous bird that inhabits pine-oak, fir and cypress forests, forest edges, shrubby clearings, gardens, pastures and cultivation areas near mid-elevation forests (from 1500 to 3350 m a.s.l., Isler & Isler 1987). It has been documented that in Guatemala it feeds on blossoms of several species of Salvia, Fuchsia, Centropogon, Penstemon and Cestrum (Skutch 1954). This bird feeds by using the upper mandible like a hook placed over the corolla tube, while piercing with the short lower mandible and introducing the tongue that, by capillarity, extracts nectar (Skutch 1954).

The natural history of this species is poorly known. There is only one nest described from the mountains of Guatemala by Skutch (1954). Lyon and Chadek (1971) and Lyon (1976) described its interaction with the shrub Penstemon kunthii, as well as with the hummingbirds and bumblebees that visit this plant in the highlands of Oaxaca, Mexico. Martínez del Río & Eguiarte (1987) mention this species as a visitant and probably pollinator of Agave salmiana in the "Valle de Mexico" (near Mexico City).

Feeding Ecology of **Diglossa baritula**.

Monthly visits to the area were carried out between October 1990 and November 1991. Each month two transects of eight mist nets each (12 meters long) were set up to catch, measure and mark individuals of D. baritula (8 hours per day beginning at dawn, 2 days in each transect). The first transect was located on a regrowth site that was burned 15 years earlier, hereafter called "non-forested area". The second transect was located in an area of dense vegetation, in a transition between humid pine forest and cloud forest (hereafter "forested area"). These two places were selected as representative of the commonest habitats in the station (Saldaña-Acosta & Jardel 1991). The location of the first net was defined by means of a randomly selected number which in turn defined the number of meters from the beginning of the transect. The other nets were then systematically separated by approximately 100 meters. Nets were located in the same places every month.

For each bird caught I measured body mass, total length, length of culmen, tail, tarsus and wing. Evidence of breeding (presence of protuberant cloaca or incubation patch) and molt were also registered. Morphological data were analyzed to assess possible differences in size between sexes or ages using principal components analysis and MANOVA (see Sokal & Rohlf 1981). Birds were individually marked using metal numbered rings or metal colored rings. Preparations of pollen collected from the head of each caught bird were made. Pollen preparations were made using a small cube of fuchsine-stained gel to rub the bird's head (throat, forehead, lores, crown, bill, chin and nostril zone). The gel was then placed on a microslide and covered. These preparations were compared with a reference collection made from pollen collected directly from the plants. Pollen identification was done by only one observer (M.C. Arizmendi). My identifications can be considered as reliable given that in a separate test in which 210 randomly chosen preparations, for which the identity of the species was not known to me, I was able to tell the correct identification in 98% of the cases.

The Plants used by D. baritula.

To determine which plant species were used by D. baritula, direct observations were made in all the plants that were in bloom during each month. In these, an observer stood in front of each blooming species (at a distance of between 1 and 4 meters) observing an individual plant (or a patch) of no more than 3.5 meters in diameter. Observations lasted up to 2 hours and ended when visitation by the robber occurred (**i.e.**, when the bird pierced at least one flower and sucked nectar from it). At least two different individuals or patches were observed (range 2-5) for each plant species blooming during each month. Individuals selected were those that bore many flowers (at least 50) and were located in places where observation was possible (e.g. not covered by vegetation). All observations were conducted in the early morning, starting half an hour after sunrise. In addition to these observations, in all blooming plant species I also surveyed flower perforations to seek for evidence of nectar robbery. This was done during the monthly censuses of flower abundance (see below for details). Pierces made by D. baritula were readily told apart from holes made by other nectar robbers, as this bird makes a hole in one side of the flower, which is accompanied by a mark left on the opposite side of the flower by the bird's upper mandible, which is used as a hook to maintain the flower stable while piercing (Colwell 1973, Skutch 1954).

For the four most abundant plant species (as defined from the monthly surveys of flower abundance, Salvia mexicana, Salvia iodantha, Ipomoea heredifolia and Lobelia laxiflora, see below for details) in which visitation by the robber could be readily quantified (by counting persistent holes on flowers), differential flower use was assessed under the null hypothesis that flowers were used according to their relative abundance. I used the number of flowers damaged as observed values to be contrasted with expected values calculated by multiplying total number of flowers damaged by the proportional abundance of flowers of each blooming species for a given month. This comparison was only possible in February because was it the month when the blooming peak of the four species occurred and sufficient flowers were available. In those four species holes made by the robber were easily and undoubtedly determined as they were permanent. In other plants, sap secretion after damage closed the holes leaving only a scratch.

Direct quantification of visitation by D. baritula was only possible for two plant species. For the rest of the plants this was not possible because of the high foraging speed of the robbers that made quantification of single visits difficult.

To measure the fluctuations in resource availability in the two areas used for bird captures, I counted the number of flowers of the different species visited by D. baritula. This survey was done by censusing a 600 m x 10 m area in each vegetation type and counting all the flowers per individual (or patch, where it was not possible to discern individuals) of all blooming species that were detected as visited by the nectar robber. Differences in the number of flowers between the two areas were assessed using a repeated measures ANOVA, with flower number at each month as the repeated measure. Data were log transformed (log X + 1).

Effects of Nectar Robbery.

In 30 individuals (chosen at random) of Salvia mexicana and 28 of Salvia iodantha I marked a pair of chalices, one from a pierced and one from a non pierced flower (chosen by random selection of individually marked flowers) in each individual, and followed them until seed production. Chalices were marked on the afternoon of the last day of duration of the flowers. (Flowers lasted four days for both plant species.) After marking, corollas were separated from chalices to ensure that no further visitation occurred. Differences in seed production were assessed with paired-sample t tests.

A second series of direct observations was conducted in order to register agonistic interactions between robbers and the other nectarivorous animals that visited the plants. I observed, during periods of 2 hours, an individual plant or a patch (< 3.5 m. diameter) from a distance that permitted full vision of the flowers (1 to 4 m). Agonistic interactions were recorded as belonging to either "fight" (when two birds faced and directed their bodies and bills against each other), or "pursuits" (when one of the birds flew rapidly towards the other, which never faced the former). The "winner" was the bird that stayed in the territory; the "loser" was the bird that flew away. Behavioral interactions were recorded during the two peaks of daily bird activity, i.e. the early morning (about half an hour after sunrise) and the afternoon (about two hours before dusk) on each month. Individual plants for these observations were selected as those that bore at least 50 flowers and were located in places where observation was satisfactory (**i.e.** not covered by vegetation).

RESULTS

Characteristics of **D. baritula** at the study site.

Diglossa baritula was found to be a resident species, with at least some birds being caught every month (Fig. 3.1A). Population numbers fluctuated widely throughout the year. In the non-forested area there were two peaks, one in January with 14 individuals caught and the other in May with 8. In the forested area there were no captures from November to May, and numbers remained rather low all year except in July, when there was a peak. The non-forested area presented more birds than the forested area throughout the year. The time course of the birds' physiological status is shown in Figure 3.2. Although no nests were observed, evidence of breeding (incubation patch or protuberant cloaca) was detected in January and August. Molt occurred throughout most of the year (Fig. 3.2).

The morphological measurements suggest that sex and age-related differences were small (Table 3.1). The means were very similar and there was very little variation for each of the variables measured (coeficient of variation ranged between 0.005 and 0.13). Moreover, a principal component analysis performed to ordinate birds according to the six morphological variables (**cf.**

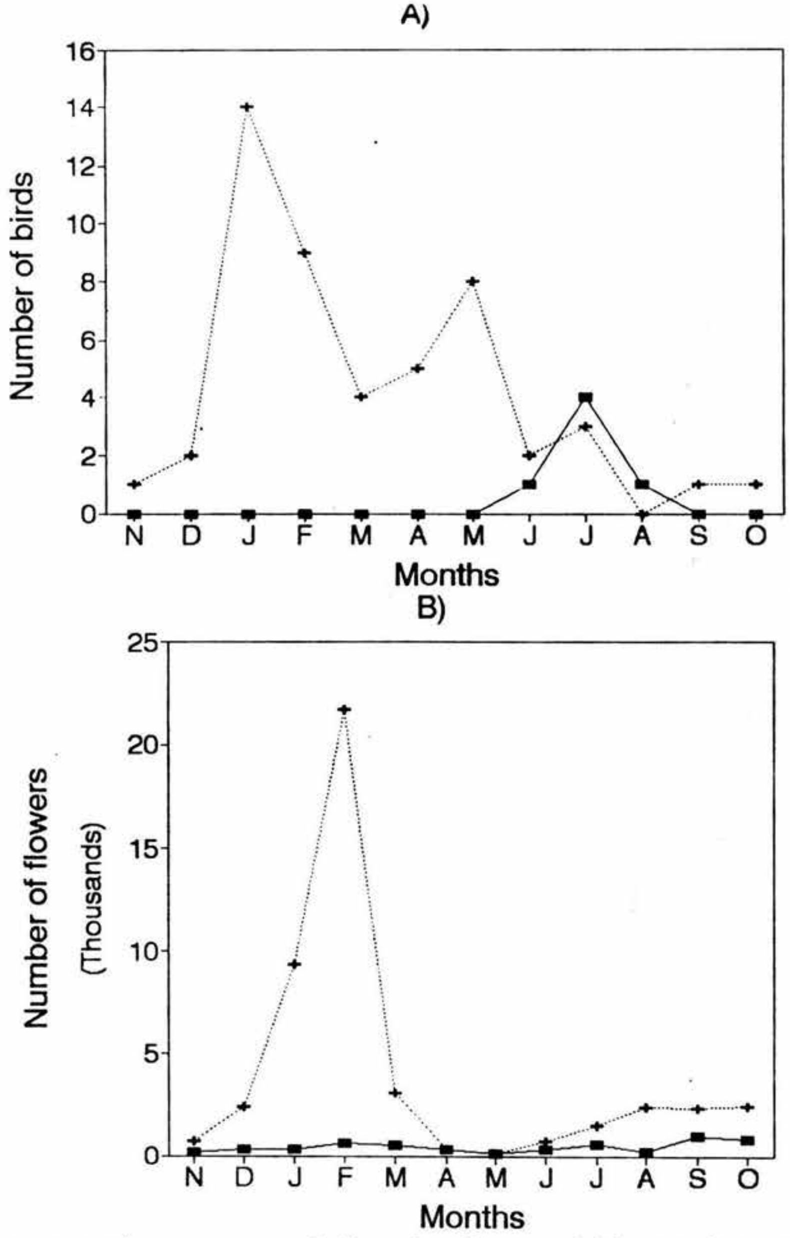

FIGURE 3.1 Time course of the abundance of the nectar robber *Diglossa baritula* (A), and of the flowers used by this bird (B) in two transects censused at Sierra de Manantlán, Jalisco, Mexico. Transects were established on a transition between pine humid forest and cloud forest (forested area, solid line ■), and a non-forested area (dotted line +).

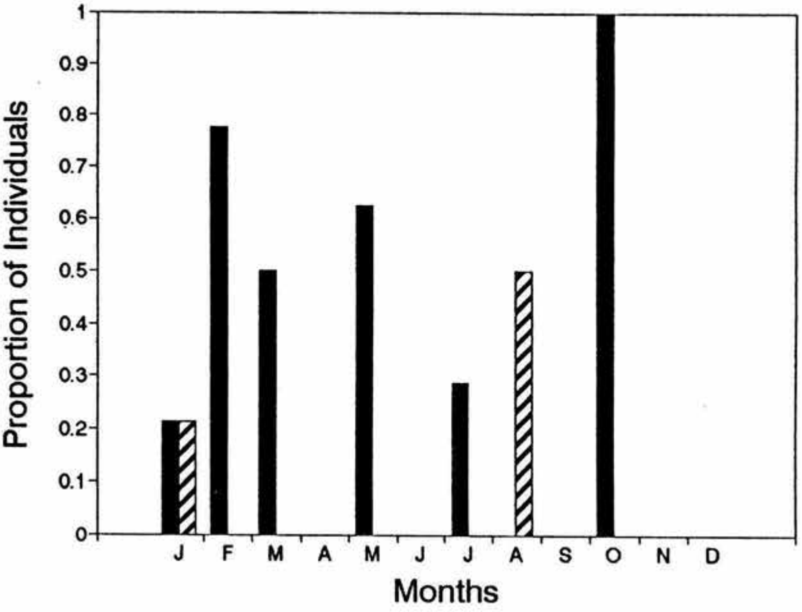

FIGURE 3.2 Period of molt (filled) and reproduction (hatched) of _D. baritula_ at Sierra de Manatlán, Jalisco, Mexico.

Table 3.1. Morphological measurements of Diglossa baritula at Sierra de Manantlán, Jalisco. Data are means and SD in parenthesis (n=10 in all cases).

	Weight (g)	Exposed Culmen (mm)	Length (mm)	Wing Chord (mm)	Tarsus (mm)	Tail (mm)
Males	8.05	9.41	104.16	52.12	16.33	44.71
	(0.66)	(0.53)	(1.57)	(1.77)	(1.37)	(2.98)
Female	7.81	9.86	104.01	52.18	15.41	43.11
	(0.61)	(0.51)	(1.57)	(3.29)	(1.78)	(5.59)
Juvenile	8.01	9.69	104.49	50.39	15.21	44.11
	(0.87)	(0.52)	(0.51)	(1.39)	(1.72)	(3.37)

Table 3.1), showed that neither sex nor age can be separated using the variables analyzed (MANOVA for the first two principal component scores (Wilks' lambda= 0.8511, P=0.674). Juveniles had plumage characteristics which were very similar to those of the females, and there was no obvious sexual dimorphism during the juvenile stages.

Diglossa baritula foraged alone or in pairs, taking between 2.5 and 10.6 seconds to pierce each flower (mean 4.78 sec; SD= 2.43, N= 30 independent observations; data from visitation to two species of flowers where visitation could be timed). On each occassion D. baritula foraged on a plant or patch it robbed, on average, 50.4 flowers (SD= 23.96; range 10-86; N=30; data for visits to all recorded plants).

From 330 visits of D. baritula recorded when hummingbirds were also present in the plant, only 18 aggressive encounters between hummingbirds and robbers could be observed. Of those, all were classified as pursuits. In 88.8% of the encounters D. baritula flew away to the nearest branch and continued visiting flowers. Only in two cases was the hummingbird successful in chasing the robber.

The plants visited by **Diglossa baritula**.

The plants visited by D. baritula to remove nectar included 16 species (Table 3.2). In addition, one shrub species (Rubus sp.) was visited mainly for fruit consumption, but also for flowers in some occasions. The average number of plant species visited per

Table 3.2. Plant species and the number of flowers (per $6000m^2$) (or inflorescences in Calliandra grandifolia and Cirsium jaliscoense) of the plants visited by Diglossa baritula at Sierra de Manantlán, Jalisco.

Species	Area+	N	D	J	F	M	A	M	J	J	A	S	O
Byttneria	F	0	0	0	0	0	0	0	0	0	0	346	0
catalpifolia	NF	0	0	0	0	0	0	0	0	247	1278	368	8
Calliandra grandifolia	NF	103	108	0	0	0	0	0	0	0	0	0	18
Castilleja	NF	-	*	*	*	-	-	-	-	-	-	-	-
Cestrum sp.	F	0	0	0	0	0	0	0	0	0	4	109	0
	NF	52	0	0	0	0	0	0	0	0	20	105	0
Cirsium jaliscoense	NF	0	0	0	8	12	18	2	0	0	0	0	0
Fuchsia	F	175	257	141	53	47	27	72	317	520	107	322	360
microphylla	NF	192	949	431	427	16	21	91	755	1182	1100	1428	2042
Fuchsia fulgens	F	0	0	0	0	0	3	2	2	19	15	10	0
Ipomoea	F	0	4	0	0	4	0	0	0	1	0	0	4
heredifolia	NF	0	37	8	15	31	12	1	0	4	0	6	9
Ipomoea	F	0	0	6	1	0	0	0	0	0	0	0	0
orizabaensis	NF	7	244	419	317	8	0	0	0	0	0	0	0
Lobelia	F	0	0	0	53	257	201	51	0	0	0	0	0
laxiflora	NF	5	71	173	381	489	266	14	0	23	0	7	0
Malvaviscus arboreus	F	26	23	11	17	4	0	0	0	11	82	39	240
Phaseolus	F	1	0	0	0	0	0	0	0	0	0	140	209
ccocineus	NF	135	0	0	0	0	0	0	0	0	0	430	353
Psittacanthus	F	*	-	-	-	-	-	*	*	*	*	*	*
ramiflorus	NF	*	-	-	-	-	-	*	*	*	*	*	*
Salvia	F	0	2	128	43	123	29	5	0	0	0	0	0
mexicana	NF	205	824	338	417	319	7	0	0	0	0	0	0
Salvia	F	0	0	0	24	75	9	0	0	0	0	0	0
iodantha	NF	24	161	8008	20106	2200	25	0	0	0	0	0	0
Tillandsia	F	-	-	*	*	-	-	-	-	-	-	-	-
Species		10	8	8	9	8	6	7	3	7	6	9	7
Flowers per month		925	2680	9663	22253	3585	618	238	1074	2007	2606	3310	3243

* plants in bloom, but not counted in the censuses;- same plants not in bloom. + vegetation area; F= Forested; NF= Non forested areas.

month was 7.3 (range 3 in June to 10 in November, SD= 1.82). The period April-August, which encompassed most of the rainy season, had a number of species visited per month below the average. The maximum number of species visited (8-10) occurred in winter, during the dry season. Transects did not differ with respect to numbers of flowers produced (Repeated measures ANOVA: $F_{(1,2)} = 1.2$; $P = 0.39$).
Regardless of species, and lumping the data for both sites, there were an average of 4350 flowers available per month and monthly abundance ranged from 238 (May) to 22253 (February). Most of the flower production occurred in the non-forested area (see Fig. 3.1B). In this area, there was a sharp increase in the number of flowers during late winter (January and February), declining at the beginning of the rainy season. During the wet season (June-October) both transects showed a slight increment in the number of flowers. The first peak of late winter in the non-forested area was due almost completely to the blooming of *Salvia iodantha* which accounted for more than 80% of the total flower production of January-February (Table 3.2). The second peak in both transects was due to the blooming of *Fuchsia microphylla*, *Phaseolus coccineus* and *Byttneria catalpifolia*. During the months when flowering was scarce, *Cirsium jaliscoense*, *Lobelia laxiflora* and *Fuchsia microphylla* were the plants that continued blooming and producing nectar, particularly in the non-forested area.

Of the six life forms of the species whose flowers were visited by *D. baritula* (Table 3.3), the predominant ones were shrubs (51%) and vines (18%; $X^2_{(5)} = 19.27$; $P < 0.005$). The species visited included one herb, one hemiparasite and one epiphyte. The flowers of these species were

Table 3.3. Life form and morphological features of the flowers visited by Diglossa baritula at Sierra de Manantlán, Jalisco.

Data for Pollinators from M.C. Arizmendi **et al.** (in prep.).

Species	Plant Life Form	Flower Shape	Color	Floral Arrangement	Pol+
Tillandsia sp.	Epiphyte	Tube	Orange	Inflorescence	H
Psittacanthus ramiflorus	Hemiparasite	Tube	Orange	Inflorescence	H
Castilleja sp.	Herb	Cup	Red	Solitary	H
Byttneria catalpifolia	Shrub	Cup	Yellow	Solitary	I
Cestrum sp.	Shrub	Tube	Yellow	Inflorescence	H-I
Cirsium jaliscoense	Shrub	Cup	Cream	Inflorescence	H-PB
Fuchsia microphylla	Shrub	Tube	Red	Solitary	H-I
Lobelia laxiflora	Shrub	Tube	Orange	Inflorescence	H
Malvaviscus arboreus	Shrub	Tube	Red	Solitary	H
Phaseolus coccineus	Shrub	Tube	Red	Solitary	H-I
Salvia iodantha	Shrub	Tube	Red	Solitary	H
Salvia mexicana	Shrub	Tube	Purple	Solitary	H
Calliandra grandifolia	Tree	Cup	Red	Inflorescence	H-PB
Fuchsia fulgens	Vine	Tube	Red	Solitary	H
Ipomoea heredifolia	Vine	Tube	Orange	Solitary	H
Ipomoea orizabaensis	Vine	Tube	Purple	Solitary	H-I

Pol+ = Pollinator: H= Hummingbird; I= Insect; PB= Perching bird mostly tube-shaped with long corollas and of varied colors, but most frequently red (7 species) and orange (4). Pale-colored flowers were the least represented (Table 3.3). *Diglossa baritula* also visited the shrub *Rubus* sp. (cup-shaped, white and solitary flowers) but it visited it only for fruit consuption. The principal visitants and probably pollinators of these plants were hummingbirds (in 15 out of 16 plant species), but insects were the main pollinators of *Byttneria catalpifolia* and also visited, to a lesser extent *Cestrum* sp., *Phaseolus coccineus* and *Ipomoea orizabaensis* (Table 3.3). Anthesis of all the flowers was diurnal.

There was a positive and significant relationship between the number of flowers and the number of birds caught in the non-forested area ($r^2_{(10)}$= 0.337; P <0.05) but in the forested area the number of flowers was not related to bird abundance ($r^2_{(10)}$= 0.0029; P >0.05). Thus for the area where the majority of the flowers were produced 34% of the variation in bird abundance was explained by flower abundance.

For the plants whose flowers were the most abundant (*Salvia mexicana*, *S. iodantha*, *Ipomoea heredifolia* and *Lobelia laxiflora*) I tested for differential use by *D. baritula* as indicated in the Methods section. The results are shown in Table 3.4. While birds used *Salvia mexicana* almost according to its flower abundances, *Salvia iodantha* was used more than expected but *Lobelia laxiflora* and *Ipomoea heredifolia* were used much less than expected by their relative flower abundances (Table 3.4).

Incidence and Effects of nectar robbery on the plants.

There was considerable variation in the percent of damaged flowers per

Table 3.4. Use by Diglossa baritula of four plant species at Sierra de Manantlán, Jalisco. Data correspond to number of pierced flowers in February.

Plant species	Observed	Expected
Salvia mexicana	375	370.13
Salvia iodantha	764	723.75
Lobelia laxiflora	4	42.07
Ipomoea heredifolia	10	17.04

chi squared= 39.66; df= 3; P<0.001

Expected values calculated according to flower proportional abundance (see text)

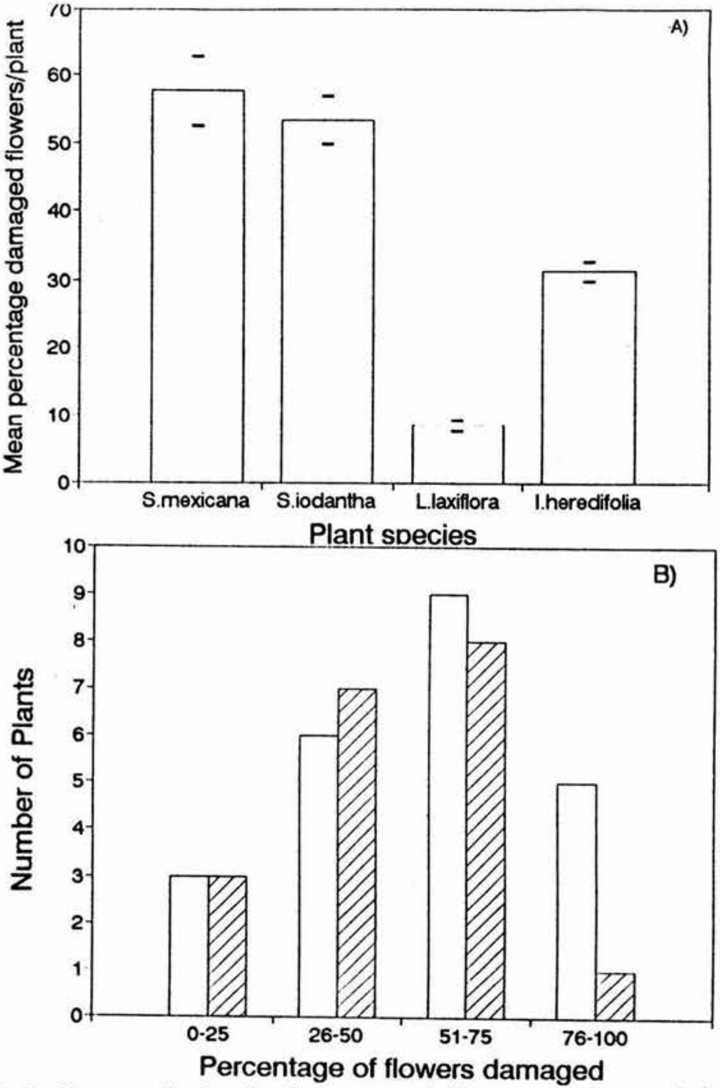

FIGURE 3.3. Mean and standard errors of the percentage of damaged flowers by *Diglossa baritula* for four plant species in Manantlán, Jalisco, México (A); Frequency distribution of flower damage by *Diglossa baritula* in the plants of *Salvia mexicana* (empty bars) and *S. iodantha* (B; hatched bars; N= 23 individuals for *S. mexicana* and 19 for *S. iodantha*).

plant among the four species assessed (Fig. 3.3A). The mean percentages were 57.6% for Salvia mexicana (N=30 individuals), and 53.4% for Salvia iodantha.

The consequences of flower piercing were assessed by counting the number of seeds produced by damaged and undamaged flowers of Salvia mexicana and S. iodantha. Plants of the genus Salvia produce from 1 to 4 seeds per flower (Sánchez 1980). For both species there was no difference between the mean number of seeds produced by damaged or undamaged flowers (Table 3.5).

Pollen grains of four plant species were found in the head of D. baritula. Two of them belonged to cup-shaped flowers pollinated by hummingbirds and perching birds (Calliandria grandifolia and Cirsium jaliscoense) and one (Byttneria catalpifolia) to insect-pollinated flowers. For the first two species D. baritula visited the flowers by the "appropriate" entrance, without piercing, and probably acted as pollinator. Bytnneria catalpifolia was visited sometimes via the correct entrance, but it was also pierced in other instances (L. Domínguez pers. com.). D. baritula may act as a pollinator of this plant too. The fourth species, the vine Psittacanthus ramiflorus, has long tube-shaped flowers and it seems doubtful that the flower piercer can both visit (for robbery) and pollinate it.

DISCUSSION

Of 16 plants visited by Diglossa baritula 15 were pollinated by hummingbirds and there was only one insect pollinated species which was visited by this robber. Thus flower piercing was a common phenomenon in this community. In all 16 species visited this bird acted as a nectar

Table 3.5. Mean number of seeds per flower (sd) produced by damaged and undamaged flowers of *Salvia mexicana* (N= 30) and *Salvia iodantha* (N= 28).

	Salvia mexicana		*Salvia iodantha*	
Damaged Flowers	1.82	(1.31)	1.72	(0.91)
Undamaged Flowers	1.55	(1.35)	1.31	(1.36)
	t= 0.477		t= 0.552	
	df= 29		df= 27	
	P>0.5		P>0.5	

robber, but in four of them pollen was found on the body of the bird, suggesting it could also act as a pollinator of these plants. However this apparently does not affect plant seed production in the species studied. Diglossa baritula pierced flowers making a very small puncture. In flowers with upper ovary such as Salvia mexicana, piercing was done about 10 mm above the ovary, skipping the protective hard tissue that covers it. Very likely such hardened tissue makes piercing difficult in this zone, thus protecting the female reproductive parts (Faegri & van der Pijl 1979, Inouye 1983). Clearly, in flowers with inferior ovary the likelyhood of damage to the female reproductive parts is even lower. Apart from the possible effect of this type of physical damage on the flowers, an indirect effect on plant reproduction could be expected if nectar robbery affected the attractiveness of flowers to pollinators or their pollination efficiency, thus reducing seed production. However, at least for the two species tested damaged and undamaged flowers produced average numbers of seeds which were statistically undistinguishable.

From the 21 plant species visited by hummingbirds in the area (M.C. Arizmendi in prep, Capítulo II), 16 (76.2%) were also used by D. baritula. Only one plant species was used by the robber and not by hummingbirds, Rubus sp., which was visited by the robber in search of fruits. Five species were visited only by hummingbirds which is significantly less than expected by chance (G test for a 2 X 2 contingency table =12.81; $P<0.001$). The use of a common resource by Diglossa baritula and hummingbirds in the study area shows that this nectar robber can be regarded as specialized in visiting hummingbird-pollinated plants (Beecher 1951, Vuilleumier 1969). This was also supported by the large number of long-tubular flowers visited by this bird. This can be considered as an adaptation to feed in flowers with high content of nectar, as it is well known that long-tubular flowers produce larger quantities of nectar than non-tubular ones (Baker & Baker 1975). The reasons for these preferences of hummingbird-pollinated flowers by *D. baritula* are not known.

The present study suggests that *D. baritula* may not necessarily be considered as a parasite of the pollination system from the plant's perspective (i.e. there was no negative effect in terms of seed production at least in two plant species). In addition, I found evidence that for four species of plants this bird has the potential to act as a pollinator. Cup-shaped flowers are usually pollinated by perching birds (Faegri & van der Pijl 1979), and it was possible that *Cirsium jaliscoana*, *Calliandra grandifolia* and *Byttneria catalpifolia* were pollinated in part by *D. baritula*. The extent to which they depend on this bird for pollination or the quality of pollination remains to be assessed experimentally. In the case of the loranthaceous hemiparasite *Psittacanthus ramiflorus*, the flowers were tubular and located in clusters. *Diglossa baritula* punctured them at the base of the corolla while it was perching in the stem of the flower cluster. When these birds attempted to pierce the flowers located toward the center of the cluster, they thrusted their head into the cluster, dusting the head and upper breast with pollen. The result of this behavior may be that central flowers become pollinated while being robbed. Graves (1982) reported that *Diglossa brunneiventris* and *Diglossa humeralis* are pollinators of *Tristerix longebracteanus* (Loranthaceae). The flowers of *Tristerix* are located on clusters directed upward and open synchronously. *Psittacanthus ramiflorus* has floral characteristics similar to those of *T.*

longebracteanus. It is therefore possible that the pollen of P. ramiflorus found in D. baritula was not only a product of chance but an indicator of pollinating (and robbing) activities of D. baritula.

The possible effect of D. baritula on hummingbirds can not be adequately evaluated from this study. Expected negative effects could not be documented as agonistic interactions between robbers and pollinators were infrequent. Coexistence, based on using a shared resource seems the prevalent phenomenon. However, the effect for both plants and hummingbirds must be assessed further under careful experimentation to attain solid conclusions about the nature of this multiple interaction. The results of this study should provide a basis for the design of such experiments.

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Capítulo IV:

El papel de los robadores de néctar en la reproducción de las plantas: un estudio de caso con *Diglossa baritula*

(enviado a Ecology)

THE ROLE OF NECTAR ROBBERS ON PLANT REPRODUCTION: A STUDY CASE WITH *Diglossa baritula*

Abstract

Nectar robbers are animals that extract the reward offered by plants to their pollinators without contacting the reproductive parts of the flower. The effect of nectar robbers upon pollination efficiency and plant reproductive output has been controversial hitherto. In this paper, the role of the primary nectar robber *Diglossa baritula* upon nectar secretion and seed set of a hermaphrodite (*Salvia mexicana*) and an andromonoecious plant species (*Fuchsia microphylla*) was assessed by means of observational and experimental studies. Both plant species are regularly pollinated by hummingbirds.

The effect of nectar robbery on nectar secretion was investigated by comparing accumulated nectar of undamaged and damaged (pierced and robbed) flowers by *D. baritula* in the field. The effect on seed set was assessed by means of enclosure experiments under field conditions, whereby individual flowers were exposed to different schedules of visitation by flower visitors: hummingbirds of varying bill size, the robber only, and the robber together with hummingbird.

The effect of the nectar robber on nectar secretion was neutral for the two plant species examined (i.e. accumulated nectar did not differ between control and robbed plants). However, in *S. mexicana*, but not in *F. microphylla*, intact flowers produced more concentrated nectar. In *S. mexicana* the number of seeds produced by flowers visited by the robber only, was similar to that produced by the least efficient pollinator, but lower than that of the other pollinators. In *F. microphylla* seed production by flowers visited by the robber only was lower than in flowers visited by all other pollinators. However, in both plant species visitation by the robber plus pollinators yielded the same number of seeds as in flowers visited by the more effective pollinators. Since under natural conditions flower visitation by the robber only is very rare, I conclude that for these two plant species, *D. baritula* must be regarded as a commensal rather than a parasite of the pollination system.

Keywords: *Diglossa baritula*; *Fuchsia microphylla*; hummingbirds; nectar-robbery; pollination efficiency; *Salvia mexicana*.

Topic sentences: Effects of nectar robbery on plant reproductive performance of two hummingbird-pollinated species.

Resumen

Los ladrones de néctar son animales que extraen la recompensa ofrecida por las plantas a sus polinizadores sin contactar las partes reproductivas de la flor. El efecto de los ladrones de néctar sobre la eficiencia en la polinización y sobre el éxito reproductivo de las plantas es un tema controvertido. En este estudio, se analizó mediante experimentos y observaciones directas, el papel del ladrón primario de néctar *Diglossa baritula* sobre la secreción de néctar y la producción de semillas de una planta hermafrodita (*Salvia mexicana*) y una andromonoica (*Fuchsia microphylla*). Las dos especies de plantas son polinizadas por colibríes.

El efecto del ladrón de néctar sobre la secreción de néctar se investigó comparando la producción acumulada de néctar en flores sin daño y dañadas (ahujereadas y robadas) por *D. baritula* en condiciones de campo. El efecto sobre la producción de semillas se estudio mediante un experimento de exclusión realizado en condiciones de campo, en donde se expuso a flores individuales a diferentes patrones de visita que incluían a colibríes de diferentes tamaños de pico, el ladrón de néctar solo, y el ladrón acompañado de una visita de uno de los colibríes.

El efecto del ladrón de néctar sobre la secreción de néctar fue neutro para ambas especies de plantas examinadas (i.e. el volumen del néctar acumulado no difirió entre flores dañadas y no dañadas). Por otro lado, en *S. mexicana* pero no en *F. microphylla*

las flores intactas produjeron néctar más concentrado. En *S*. *mexicana* el número de semillas producidas por las flores visitadas solo por el ladrón fue similar al producido por una visita del polinizador menos eficiente, pero menos al producido por todos los demás polinizadores. En *F*. *microphylla* la producción de semillas de las flores visitadas solo por el ladrón fue menor que la de todos los demás tratamientos. De cualquier forma, para ambas especies de plantas el rendimiento producido por flores visitadas por un polinizador y el ladrón fue indistinguible al producido por los polinizadores más eficientes. Sabiendo que en condiciones naturales la visita a una flor por solamente el ladrón es un evento raro, se concluye que para estas dos especies de plantas, *D*. *baritula* puede ser considerado más como un comensal del sistema que como un parásito.

INTRODUCTION

The effects of illegitimate flower visitors and nectar robbers (Inouye 1983) on plant fitness are controversial. Some authors argue that the effect is positive because by depleting or reducing nectar, robbers force pollinators to move more among flowers. This could result in more inter-plant pollen movement and consequently higher outcrossing rates and seed production (Hawkins 1961, Heinrich and Raven 1972, Soberón and Martínez del Río 1985). Also, positive effects are reported for some bees that pollinate flowers while piercing their corollas, presumably as a result of flower movement during the puncturing and robbery (Koeman-Kwak 1973). Negative effects have been reported by several authors studying pollination systems from different points of view. McDade and Kinsman (1980) evaluated the effect of nectar robbers in two hummingbird-pollinated herbs (Aphelandra golfodulcensis and Justicia aurea). They found that robbers reduced both nectar production and seed-set in flowers damaged by them. Roubick (1982) reported that Trigona ferricauda, the nectar robber of Pavonia dasypetala, chases away the pollinator Phaethornis superciliosus, thus preventing the flowers from being pollinated and no seed production occurred.

Additionally, legitimate visitors vary in their efficiency to pollinate flowers and produce seeds (Campbell 1985, Cruden 1972, Herrera 1988, Horvitz and Schemske 1984, Primack and Silander 1975, Schemske and Horvitz 1984). Furthermore some of these visitors can be regarded as robbers as their net effect is for the plant to produce no seeds. Despite the evolutionary relevance of the differential effectiveness of pollinators, there are only a few studies in which the effects of different pollinators for plant fitness in field conditions have been investigated (Cruden 1972, Herrera 1987, Primack and Silander 1975, Schemske and Horvitz 1984). Most of these studies have demonstrated that the differences in pollination efficiency can be attributable to variation in the size of the visitors or to 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). The interaction of plants with robbers and pollinators may be influenced by factors such as morphology of the visitors, the plant's compatibility system, availability and quality of rewards, and spatio-temporal variations in the components of the pollination system (Herrera 1988, Horvitz and Schemske 1990, Schemske and Horvitz 1984). Therefore, the classification of floral visitors as "robbers" and "pollinators" most be taken with caution as in some cases robbers can act as pollinators (see for example, Graves 1982, Hawkins 1961) and pollinators can act as robbers or illegitimate visitors (see for example, Herrera 1988, Schemske and Horvitz 1984). Given the varied nature of the effects of nectar robbery, it is clear that more studies with careful manipulations are needed. The purpose 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). The specific questions I addressed in this study were: 1) What are relative abundances of both pollinating hummingbirds and nectar robbers; 2) What is the frequency of nectar robbery under field conditions; 3) Do nectar robbers affect the patterns of nectar secretion and seed production, and finally 5) Does the impact of nectar robbery on plant reproduction change as a function of the composition of the pollinator guild.

These two plant species were selected because they were the most common hummingbird-pollinated plants at our study site. They have similar flower morphology (Arizmendi 1994), share many species of flower visitors (both hummingbirds and the nectar robber D. baritula), and have contrasting breeding systems.

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. The area is located in the highlands of the Mexican States of Jalisco and Colima, in the Sierra de Manantlán, about 50 km east of the Pacific Coast in western Mexico (19° 35' N; 104° 16' W). The Laboratorio Natural Las Joyas is a 1245-ha preserve, situated at 1952 meters above sea level. Annual mean precipitation is 1610 mm, with most of the rain falling between June and October. Mean annual temperature is 14.6°C with very few days a year with temperatures below the freezing point. The vegetation is constituted by a complex mosaic of humid coniferous forest, pine-oak forest, patches of cloud forest located at ravines, and secondary vegetation product of either burning or agricultural, abandoned areas. A detailed analysis of the structure and composition of vegetation is given by Guzmán (1985), Saldaña-Acosta and Jardel (1991) and Vázquez **et al.** (1990).

Species Studied

At our study site D. baritula is the main avian nectar robber of hummingbird-pollinated plants, taking nectar of 76% of the plants visited by them (Arizmendi 1994). D. baritula feeds by using the upper mandible like a hook over the corolla tube, piercing with the short lower mandible and introducing the tongue that, by capillarity, extracts nectar (Skutch 1954). The hummingbird community in the area is composed of seventeen species (Arizmendi 1994), four of which are residents, six are winter visitors, two are summer visitors that stay in the area more than half of the year and five are summer visitors.

Salvia mexicana L. is a self-compatible perennial herb that grows in humid highland forests in Mexico. It is visited and pollinated by hummingbirds. Flowers are hermaphrodite with long purple tubes (mean length 29.8 mm; SD= 1.49; N= 46). Blooming is concentrated from November to March.

Fuchsia microphylla H.B.K. is a self-compatible androdioecious shrub that grows in pine, pine-oak and cloud forests in the highlands from Central Mexico to Panama. It is visited and pollinated by hummingbirds and bumblebees. The blooming of F. microphylla at Manantlán is spread through the year with a peak from August to October and another in December to January (Arizmendi 1994). Male flowers are always longer (mean 12.03 ± 1.37 mm; N=50) and brighter than hermaphrodite ones (mean 10.73 ± 1.26 mm; N=50). At the study site individual flowers last for five days.

Field Procedures

Flower visitors

Direct observations of avian flower visitors were made in each of five patches of flowering plants for the two studied plant species. Observations were carried out half an hour after sunrise and half an hour before dusk by one observer who stood in front of each patch. Patches were selected in places of high abundance of flowers (100 to 400 open flowers each) and where visibility was high. This way all the patch area, that never exceeded 3.5 m^2, could easily be observed from a distance of 1 to 4 m. Observations lasted two hours. For each visit I registered the species of all flower-visitors, the number of flowers probed and the duration of each visit. The species of the most common visitants (defined as the ones that visited the largest number of flowers) were chosen for the experimental manipulations described below. Observations were repeated during two days for both plant species, in the morning and in the afternoon.

Damage frequency and position on flowers

Damage frequency and its position on the flowers were measured to detect possible damage to the reproductive parts (ovaries) of the flower made by the robber when piercing.

The frequency of damage was measured in ten individuals chosen at random from each plant species. For the ten chosen plants all the flowers were counted and inspected, and the ratio of damaged to non-damaged flowers was calculated. In the same flowers, I measured the position of the piercing (distance in relation to the calix).

Effects on nectar secretion

A sample of 140 and 280 first-day flowers of *S. mexicana* and *F. microphylla*, respectively, was chosen at random (by marking all the flowers in the different individuals and calling random numbers from a calculator) from a total of 20 plants of *S. mexicana* and 10 plants of *F. microphylla*. For each species, half of the flowers (chosen at random) were pierced experimentally by *D. baritula*. This was achieved by holding the bird by the feet in front of the flowers and waiting until it pierced the corolla and extracted nectar. Those flowers were then marked with thin plastic numbered rings. Flowers for which this procedure was not satisfactorily achieved were discarded. The remaining half of the flowers were only marked and used as control flowers. Nectar was not removed manually from control flowers because this procedure caused damage to reproductive parts. After marking, control and pierced flowers were bagged using mosquito netting bags. On the following day after treatment application (approximately 24 hours after), a subsample of ten damaged and ten undamaged flowers was randomly selected every two hours from dawn to dusk. For each flower I measured the amount of nectar accumulated with calibrated microcapillary tubes, and nectar concentration was measured using a hand-held refractometer (ERMA 101190-32). For *F. microphylla* both male (*N*=140) and hermaphrodite flowers (*N*=140) were used to compare nectar accumulation in damaged and undamaged flowers of both sexes.

Effects of nectar robbery and composition of the pollinator guild on plant seed set

In order to assess the effect of different species of hummingbirds and the nectar robber *D. baritula* on seed set of *S. mexicana*, I performed an experiment where the order of visitation (robber, pollinator) and the species of hummingbird were controlled. In these experiments 30 caged plants (see below for details) of similar size, and captive birds belonging to four species of hummingbirds and *D. baritula* were used. For each shrub I marked eight randomly chosen flower buds with individual tags (thin plastic numbered rings) around the pedicel. At anthesis, each flower within a study plant was assigned randomly to one of the following treatments:

1-4. I tested pollinator efficiency by offering flowers (one flower to each hummingbird species in each study plant) to four species of hummingbirds of different bill size: *Selasphorus* rufus<Hylocharis leucotis<Lampornis amethysthinus<Eugenes fulgens),

5. To test for the effect of the robber, I permitted only one visit of D. baritula,

6-7. In order to look for indirect interactive effects, I allowed one visit of the nectar robber and then one of H. leucotis (the most frequent flower visitor of both plant species), and viceversa,

8. Finally, to assess for automatic self-pollination, I bagged flowers individually, excluding both pollinators and robbers.

Similar procedures were used in the case of F. microphylla, but treatments were different with regard to the identity of pollinators. In this case, to assess pollinator efficiency, only two hummingbirds were used: Atthis heloisa and H. leucotis. These were the smallest of all the hummingbirds that occurred in the area and among the most common visitors to F. microphylla. Treatments involving D. baritula were equal to those performed with S. mexicana. An additional treatment of outcrossed hand-pollination was used to test for pollinator limitation. For this species I used 16 replicates (i.e. 1 flower per treatment in each of 16 plants) of each treatment.

For each study plant treatments were applied as follows. Once flower buds were assigned to a given treatment, they were bagged (with mosquito net bags) and left so until anthesis. At anthesis, a mosquito net cage (5x5x2m) was placed covering all the shrub, and one or more unused neighboring flowering shrubs.

Next I unbagged one of each of the experimental flowers assigned to a particular treatment, and released a bird into the cage (pollinator and/or nectar robber, depending on treatment) and allowed it to visit the targeted flower and other flowers from the other shrubs enclosed. This procedure assured that birds visiting target flowers carried pollen on their bodies. Once the target flower was visited, I removed the bird and rebagged the flower. When all treatments were completed I waited for fruit maturation, and fruits were collected and the number of seeds per fruit were counted.

Both hummingbird and D. baritula individuals were captured at least four days previous to the experimental day and kept in individual cages. Birds were fed using artificial feeders and a 20% solution of sugar. Fruit flies were supplied in order to balance diet with proteins.

For both plant species, a pollination efficiency score (PES) was calculated for each species of avian flower visitor. Seed production per visit has been defined as the "quality" component of pollination efficiency (Herrera 1987). This factor, multiplied by the "quantity" component defines the PES of a particular pollinator. I used the percentage of visited flowers as the quantity component and the number of seeds produced per visit as the quality component. The PES is intended to compare relative pollination efficiencies among flower visitors for each of both plant species studied.

RESULTS

Salvia mexicana

Visiting Patterns

Salvia mexicana was visited by five species of hummingbirds and the nectar robber D. baritula (Table 4.1). All hummingbird species did legitimate visits to flowers, and therefore they can be considered as potential pollinators for this species. A single flower can be repeatedly visited by hummingbirds, while visits by avian nectar robbers occurs only once. The ratio of the number of flowers visited by hummingbirds to those visited by D. baritula was 7.36 (from a total of 3706 observed visits).

Damage frequency and position in flowers

A total of 92% of the flowers were pierced by D. baritula in the field. Piercing was done on the calix at an average distance of 5.43 mm from the base of the flower ($SD=2.24$; $N=46$) where the ovaries are located. In no case was damage to the floral reproductive parts (ovaries) detected.

Effects on nectar accumulation

The amount of nectar accumulated was similar in robbed and intact flowers (Fig. 4.1A). There was a considerable degree of variation among flowers and the differences between robbed and intact flowers were not significant (ANOVA, $F_{(1,126)}=4.46$, $P>0.10$). There was a significant increase in the amount of nectar per flower through time, which reached a maximum at approximately 15:30 h (Fig 1A; ANOVA, $F_{(6,126)}=8.34$, $P<0.05$). Nectar of intact flowers was significantly more concentrated than that of pierced flowers

Table 4.1. Bird species, percentage of flowers visited and residence status of the visitants of Salvia mexicana (a) and Fuchsia microphylla (b) at Sierra de Manantlán, Jalisco.

a) Salvia mexicana

Species	Residence Status	Activity	% Flowers visited
Amazilia beryllina	Summer visitor*	Pollinator	6.1
Eugenes fulgens	Resident	Pollinator	0.3
Hylocharis leucotis	Resident	Pollinator	27.2
Lampornis amethystinus	Resident	Pollinator	34.1
Selasphorus rufus	Winter visitor	Pollinator	15.1
Diglossa baritula	Resident	Robber	17.2

b) Fuchsia microphylla

Species	Residence Status	Activity	% Flowers visited
Atthis heloisa	Resident	Pollinator	7.5
Hylocharis leucotis	Resident	Pollinator	32.7
Selasphorus rufus	Winter visitor	Pollinator	48.2
Diglossa baritula	Resident	Robber	11.6

* summer visitor of long stay.

as showed by ANOVA ($\underline{F}_{(1,126)}$=38.14, $\underline{P}$<0.001; Fig. 4.1B).

Effect of nectar robbery on seed production

The effects on seed production of individual plants and pollination treatments were assessed using a contingency analyses 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 seeds per treatment), error was declared as Poisson (Healy 1988). Seed production among plants did not differ significantly ($\underline{X}^2_{(29)}$=29.98, $\underline{P}$>0.25). In contrast, there were significant differences on seed production of S. mexicana among pollination treatments ($\underline{X}^2_{(7)}$=102.52, $\underline{P}$<0.001). The interaction between plant and treatment was no significant ($\underline{X}^2_{(202)}$=195.4, $\underline{P}$>0.1). Although automatic self-pollination was the treatment producing the lowest number of seeds, this treatment did not differ from that of visitation by D. baritula (Table 4.2). Flowers visited by the robber produced a similar number of seeds than that produced by E. fulgens, but differed from all other treatments (Table 4.2). With the exception of both extremes of bill-size (H. leucotis and E. fulgens), all treatments involving hummingbird visitation produced numbers of seeds which were statistically indistinguishable (Table 4.2).

Regarding pollination efficiency, H. leucotis and L. amethysthinus were the most efficient pollinators (PES=68.81 and 64.41, respectively). Selasphorus rufus was almost half as efficient (PES=33.67), and E. fulgens was the least efficient

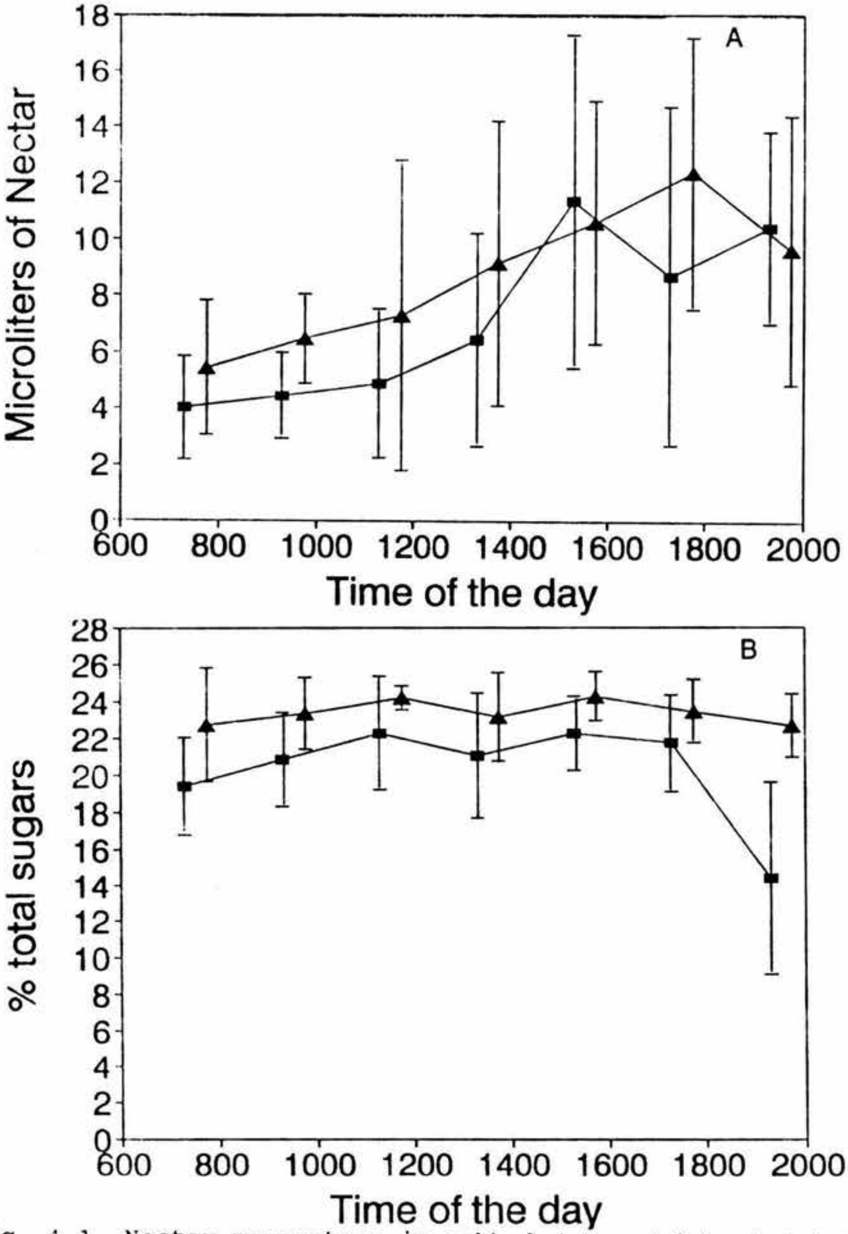

Fig. 4.1. Nectar parameters in robbed (▲) and intact (■) flowers of Salvia mexicana. A) Nectar volume; B) nectar concentration. Data are means ± 1 standard deviation ($\underline{N}$=10). Data points are slightly displaced for clarity.

pollinator (PES=0.43). Unexpectedly, the nectar robber yielded a 30 times greater PES (15.91) than that of E. fulgens.

Fuchsia microphylla

Visiting patterns

Flowers of F. microphylla were visited by three species of hummingbirds, by D. baritula (Table 4.1B) and by bumblebees (Bombus sp.). Both hummingbirds and bumblebees were legitimate flower visitors of this species. As was the case for S. mexicana, there was only one event of robbing per flower. The ratio between the number of flowers visited by hummingbirds to flowers visited by the robber was 7.5 (48 visited by the robber out of a total of 365 flowers visited by hummingbirds). Although male and hermaphrodite flowers received almost the same number of visits (185 to male flowers, and 180 to hermaphrodite ones), hermaphrodite flowers were significantly less robbed ($X^2_{(1)}$=20.65, P>0.001). In male flowers the ratio was 4.74 (39 male flowers damaged out of 185 visited by hummingbirds) while in hermaphrodite flowers it was 20 (9 hermaphrodite flowers visited by the flower robber out of 180 visited by hummingbirds).

Damage frequency and position in flowers

Holes were made in the basis of the corolla tube (mean distance from ovaries in hermaphrodite flowers 3.2 mm, SD= 0.24, N= 50), and were present in 26% of the hermaphrodite flowers and 43% of the male flowers (15 males plants, 299 flowers; 15 hermaphrodite plants, 189 flowers). In no hermaphrodite flower was damage to the ovary detected.

Table 4.2. Mean number of seeds produced by flowers of *Salvia mexicana* under different experimental treatments (replicates=30). Means with the same letter are not significantly different (Tukey's Test *P*>0.05).

Treatment	Mean	SD	
Automatic self-pollination	0.13	0.43	A
Diglossa baritula	0.93	1.15	A B
Eugenes fulgens	1.43	1.31	B C
Pollination + *D. baritula*	1.73	1.31	C D
Lampornis amethysthinus	1.90	1.30	C D
D. baritula + pollination	1.90	1.37	C D
Selasphorus rufus	2.23	1.33	C D
Hylocharis leucotis	2.53	1.15	D

Effects on nectar accumulation

Damage made by the nectar robber did not have a significant effect either on nectar quantity ($F_{(1,262)}=0.14$, $P>0.05$) or on its concentration ($F_{(1,262)}=3.91$, $P>0.05$). In contrast, there was a marked difference between hermaphrodite and male plants in both quantity ($F_{(1,262)}=23.61$, $P<0.001$) and concentration of nectar ($F_{(1,262)}=29.41$, $P<0.001$). Male flowers produced more nectar with higher concentration of sugars (Fig. 4.2). There were no differences between hours either in the quantity ($F_{(6,262)}=1.41$, $P>0.05$) or quality of nectar ($F_{(6,262)}=1.21$, $P>0.05$). Interactions among factors were not significant ($P>0.1$ in all cases).

Effect of nectar robbery on seed production

Statistical analyses were similar to those used for S. mexicana (see above). Seed production among plants did not differ significantly ($X^2_{(15)}=13.6$, $P>0.05$). In contrast, there were significant differences on seed production among pollination treatments ($X^2_{(6)}=675.4$, $P<0.001$). The interaction plant x treatment was also significant ($X^2_{(89)}=300.8$, $P<0.001$). Visitation by D. baritula alone produced the lowest number of seeds, statistically different from all other treatments (Table 4.3). Automatic self-pollination produced also a small number of seeds, which was significantly lower than treatments involving hummingbird visitation and manual outcross pollination. There were no differences among treatments that included visitation by hummingbirds (Table 4.3). Manual outcross pollination was the treatment producing the highest number of seeds. With the

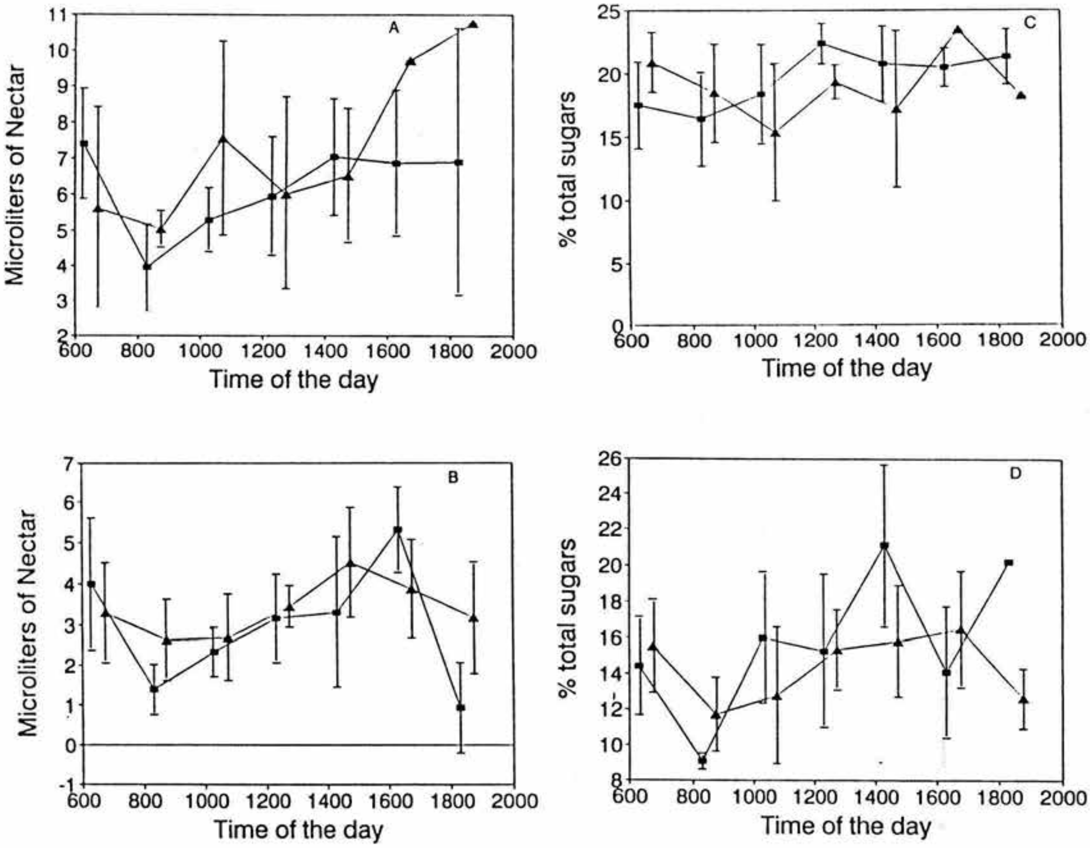

Fig. 4.2. Nectar parameters in robbed (▲) and intact (■) flowers of <u>Fuchsia</u> <u>microphylla</u>: Nectar volume in male (A) and hermaphrodite (B) flowers; nectar concentration in male (C) and hermaphrodite (D) flowers. Data are means ± 1 standard deviation (N=10).

exception of the H. leucotis and H. leucotis+D. baritula treatments, this value significantly differed from all other treatments.

The above results suggest that the potential negative effect of D. baritula on seed production of F. microphylla depends on the probability a hermaphrodite flower has to be visited only by the nectar robber.

Pollination efficiency scores for the avian flower visitors of F. microphylla indicated 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 A. heloisa.

DISCUSSION

The effect of the nectar robber D. baritula on the reproductive output of the two studied plant species varied depending on intrinsic features of each plant and also on the presence of other flower visitors. Nectar concentration, but not nectar production of S. mexicana was affected by nectar robbery: damaged flowers produced more diluted nectar than that of undamaged flowers. This reduction could be a direct consequence of damage to secretion tissues, or a plant response to invest less in already-damaged flowers. Nonetheless, our results indicate that the subsequent consequences of less concentrated nectar on plant reproductive success are negligible (see below). In fact, the activities of D. baritula on S. mexicana flowers had no negative effect on seed production, and this visitor may be even

Table 4.3. Mean number of seeds produced by flowers of *Fuchsia microphylla* under different experimental treatments (replicates=21). Means with the same letter are not significantly different (Tukey's Test *P*>0.05).

Treatment	Mean	SD				
Diglossa baritula	0.15	0.48	A			
Automatic self-pollination	4.61	7.19		B		
Atthis heloisa	13.10	10.76			C	
D. baritula + Pollination	13.63	11.52			C	
Pollination + *D. baritula*	15.88	10.10			C	D
Hylocharis leucotis	16.47	9.46			C	D
Outcross pollination	19.22	8.67				D

considered as a low-efficiency pollinator. In contrast, from the point of view of the hummingbirds, this reduction could have negative consequences as they might have to invest more time and visit more flowers to meet their energetic requirements (Inouye 1983).

On the other hand, in terms of nectar secretion, D. baritula can be regarded as a commensal of F. microphylla, as neither nectar volume nor nectar concentration were affected. The single negative effect on seed production found in this study occurred when D. baritula was the only flower visitor of F. microphylla flowers. Under these circumstances seed production had a 30-fold reduction with respect to automatic self-pollination. However, two lines of evidence indicate that this situation is uncommon under field conditions. First, at our study site hummingbirds greatly outnumbered nectar robbers, and thus a robbed flower has a high probability of being revisited by hummingbirds (Arizmendi 1994). Second, there were no differences in seed production among treatments involving visits by hummingbirds plus D. baritula (see Table 3). Therefore, although D. baritula has the potential to reduce the production of seeds of F. microphylla, this potential is precluded by the interaction with other flower visitors.

This study demonstrates that the effect of D. baritula on the reproductive success of the studied species varies from that of a low-efficiency mutualism to almost neutrality. This underscores the necessity of studying the effect of each flower visitor on different plant species (Herrera 1988, Horvitz and

Schemske 1988, Schemske and Horvitz 1988), as they can be playing a role ranging from parasitism to mutualism.

The efficiency of hummingbirds as pollinators of S. mexicana was variable and related to bill length. E. fulgens, the species with the longer bill was the poorest pollinator with a similar efficiency to that of D. baritula. Although S. mexicana is a plant that can produce seeds in the absence of pollinators, pollinator-visited flowers produced more seeds than non-visited ones. Hummingbirds with the shortest bill were associated to the highest seed production per flower. H. 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=2.38). Therefore, during their visits, these birds' foreheads effectively contact the anthers of the flowers. Pollination by the larger hummingbird E. fulgens significantly produced fewer seeds per flower than H. leucotis. The exposed culmen of E. fulgens is around 28 mm (SD=0.94), which added to the length of the tongue (Johnsgard 1983), almost doubles the size of corolla tube of S. mexicana. This means that when visiting, the pollen of S. mexicana is deposited on the bill, rather than in the forehead as is the case with the smaller birds (M.C. Arizmendi, pers. obs.). Hummingbird bills are covered by a waxy substance (Johnsgard 1983), and for that reason pollen falls off easily and quickly, resulting in a more uncertain pollination. Pollination by L. amethysthinus, the medium sized bill hummingbird, 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 number of seeds. This result could be a consequence of the reduced variance in bill length among the flower visitors of *F. microphylla* when compared with those of *S. mexicana* ($s^2=6.92$ for *F. microphylla* and $s^2=16.51$ for *S. mexicana*; $F_{(49,29)}=2.38$, $P<0.002$).

As stated by Schemske and Horvitz (1984), variation among pollinators in their ability to produce seeds is a precondition to pollinator specialization. Such 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 for both plant species. This hummingbird's efficiency was 160 and 309 times higher than that of the least efficient flower visitors of *S. mexicana* and *F. microphylla*. Thus, the ecological conditions that could favor pollinator specialization are met for both plant species. These results contrast with the general view of hummingbird-pollinated plants as systems visited by a diverse array of pollinator species (i.e. Wolf et al. 1976, Feinsinger 1976, 1978, Stiles 1980, Jordano 1987). The lack of specialization in hummingbird-pollinated systems so far studied could have at least two explanations: 1) from the plant's perspective, all flower visitors are equivalent in terms of their pollination efficiency, and 2) the specific composition of the pollinator guild varies through time and space, bringing about a spatio-temporal shift in the rank of the different hummingbird species' pollination efficiency. My results are compatible with the second explanation. Given the ubiquitous variation in specific composition and abundance of pollinators in time and space (Feinsinger and Colwell 1978, Arizmendi 1990, 1994), I suspect that the latter is a more typical situation for plant-hummingbird pollination systems.

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Conclusiones

Los resultados obtenidos en este estudio hacen evidente que el papel de los ladrones de néctar en los sistemas mutualistas de polinización biótica no puede ser generalizado pues, depende de muchos factores intrínsecos a las especies interactuantes (Astatt & Rundel 1982, Horvitz & Schemske 1990). De esta forma, *Diglossa baritula* puede ser considerada como i) posible polinizador directo de un grupo de especies de plantas; ii) polinizador indirecto (polinizando accidentalmente) de otro grupo de plantas; así como iii) posible competidor de los polinizadores. Su papel en la comunidad parece ser el de comensal si se analiza sólo el efecto bajo condiciones naturales para dos especies de plantas (*Salvia mexicana* y *Salvia iodantha*; Capítulo III). Para las dos especies de plantas estudiadas experimentalmente (*Salvia mexicana* y *Fuchsia microphylla*; Capítulo IV), es evidente que *Diglossa baritula* representa solamente el papel de un comensal del sistema siendo los efectos de su presencia, desde el punto de vista de la adecuación de la plantas, nulos, siempre y cuando se presenten visitas mezcladas del ladrón y del polinizador a una misma flor. En ausencia de los polinizadores la visita de *D. baritula* produce efectos neutros en el caso de *Salvia mexicana*, y negativos en el caso de *Fuchsia microphylla*. En estas condiciones podría representar el papel de un comensal o de un parásito respectivamente. Las posibles causas de su efecto negativo sobre la producción de semillas de *F. microphylla* no se conocen, ya que no produce daño a los órganos reproductivos de las plantas, quedando esto demostrado con el alto número de semillas que se producen al presentarse polinización y visita del ladrón. Al parecer, en ausencia de polinización, el daño producido por el ladrón es más pronunciado, debido posiblemente a la baja calidad de las semillas producidas por auto-polinización, que probablemente lleven a la planta a invertir menos en flores dañadas y no polinizadas, con lo que el índice de aborción podría aumentar.

De la misma forma se puede decir que su efecto es nulo si lo que se considera es la producción de néctar de _Fuchsia microphylla_ y la producción de semillas en condiciones naturales de las dos especies analizadas (capítulo II, _Salvia mexicana_ y _Salvia iodantha_). Por otro lado, las flores de _S. mexicana_ producen néctar más diluido en presencia del ladrón, lo que nos lleva a pensar en posibles efectos negativos sobre los polnizadores que, al encontrar flores cuyo néctar tiene menos azúcares, tienen que invertir un tiempo mayor en forrajear para satisfacer sus requerimientos energéticos.

El papel de _D. baritula_ como competidor de los colibríes debe ser evaluado de manera experimental para poder obtener conclusiones precisas al respecto; los datos presentados aquí aportan evidencias indirectas de la importancia del fenómeno. De cualquier forma, para cada especie de colibrí, la presencia del ladrón puede compararse con la presencia de cualquier otra especie de colibrí, e incluso resultar menos negativa, dado que la frecuencia de interacciones antagónicas entre colibríes es mucho mayor que entre un colibrí y una _D. baritula_.

En este trabajo se encontró que para la mayoría de las plantas, Diglossa baritula puede ser considerada más un comensal o un polinizador poco eficiente que un ladrón o parásito del sistema. Este resultado puede compararse con los estudios anteriores (Fig. 5.1), resultando que en total existen más plantas en donde se han documentado efectos positivos o neutros que aquellas en donde se encontraron disminuciones en la adecuación o en parámetros como la producción de néctar.

El papel de Diglossa baritula como comensal o incluso como polinizador "poco eficiente" en los sistemas mutualistas colibríes-plantas podría representar el resultado evolutivo de una presión de selección negativa tanto para las plantas como para los polinizadores, que los llevó a desarrollar mecanismos "defensivos" para disminuir el daño y poder coexistir con los ladrones. Para las plantas, uno de estos mecanismos podría ser el presentar el ovario en partes no accesibles al ladrón así como mecanismos de producción compensatoria de néctar, de manera que no se vea afectada por la presencia de los ladrones (Inouye 1983). La presencia de altas densidades de polinizadores en relación con los ladrones, puede representar otra forma en la que un sistema de polinización biótica pueda coexistir con ladrones de néctar (Soberón & Martínez del Río 1985).

Los efectos del robo de néctar sobre los sistemas mutualistas de polinización biótica han sido documentados en un

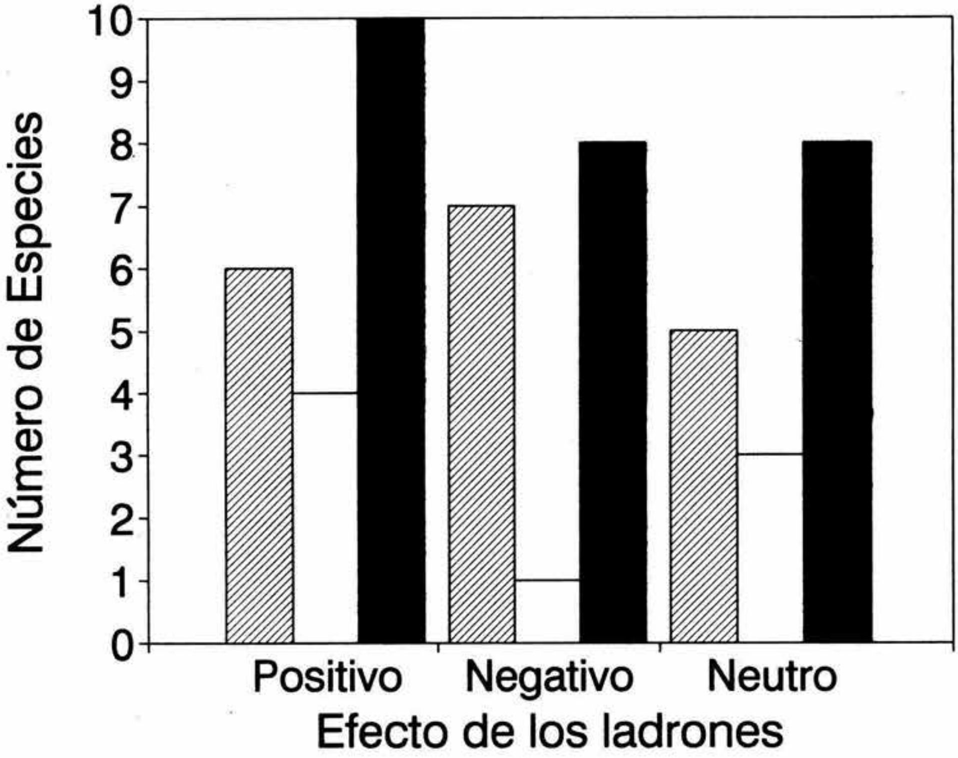

FIGURA 5.1. Número de especies de plantas en donde se documentaron efectos positivos, negativos y neutros en la literatura (barras achuradas), en este estudio (barras vacías) y en total (barras negras).

número limitado de plantas (Tabla 5.1). Muchos de los trabajos publicados solamente mencionan a los ladrones de néctar como presentes en sistemas de plantas polinizadas bióticamente, y es por eso que los efectos sobre el sistema son aún un tema controvertido. Inouye (1983), haciendo una revisión del tema, concluyó que existen trabajos que apoyan todos los posibles resultados teóricos del efecto del robo de néctar, es decir,que los efectos sean positivos, negativos o que no existan efectos sobre el sistema. La mejor forma en que se puede demostrar la dirección del efecto de ladrones de néctar sobre los sistemas biológicos es mediante experimentos, manipulando las visitas florales de manera que se tengan exclusiones múltiples. Este tratamiento experimental se ha seguido en un número muy limitado de casos que involucran como ladrones de néctar a insectos, cuya manipulación experimental ha sido usada en los últimos años, en este y otros campos de la ecología (Fritz 1981, Galen 1983, Gill 1982, Mc Dade & Kinsman 1980, Normet 1988, Roubick 1982, Zimmerman & Cook 1981). Los resultados de estos trabajos son variados y no apuntan en una sola dirección, existiendo algunos que concluyen que el efecto es negativo sobre la producción de semillas (Fritz 1981, Galen 1983, Mc Dade & Kinsman 1980), otros que encontraron efectos neutros sobre este parámetro (Norment 1988, Zimmerman & Cook 1985), mientras que los efectos positivos se han mostrado cuando los ladrones, al visitar, accidentalmente tienen contacto con las partes reproductivas de las plantas (Graves 1982, Koeman-kwak 1973). En relación a los efectos sobre

Tabla 5.1. Trabajos en donde se han reportado efectos de los ladrones de néctar sobre las plantas y sus polinizadores.

Especie	Polinizador	Robador	Efecto	Fuente
Aphelandra golfodulcensis *(Selva Alta)*	*Phaethornis superciliosus* *Phaethornis longuemareus* *Heliotrix barroti*	*Xylocopa sp.* *Trigona sp.* *Heliotrix barroti* *Phaethornis longuemareus* *Thalurania furcata* *Coereba flabeola* *Amazilia tzacatl*	**Negativo (experimental) semillas**	**McDade et al (1980)**
Aquilegia sp.		*Apis mellifera* *Bombus sp* *Lasioglossum*	**Positivo**	**Macior, 1966**
Asclepias syriaca	*Mariposas*	*Lasius neoniger* *Tapinoma sessile*	**Negativo** **Neutro**	**Fritz et al, 1981**
Centropogon valerii *(Bosque Templado)*	*Colibri thalassinus* *Eugenes fulgens* *Panterpe insignis*	*Rhinoseius colwelli* *Selasphorus flammula* *Diglossa plumbea* *Bombus sp*	**Negativo**	**Colwell, 1974**
Frasera speciosa	*Bombus centralis* *Ctenicerca fallax* *Euxoa lewisi* *Bombus frigidus* *Eulaemus synthridis* Moscas	*Formica neorufibarba*	**-Neutro semillas** **-Negativo nectar**	**Norment, 1988**
Impatiens capensis	*Vespula mellifera* *Bombus vagans* *Bombus impatiens* *Apis mellifera*	*Auglochlora pura* *Vespula mellifera* *Crematogaster sp.* *Bombus affinis* *Apis mellifera* *Auglochloropsis metalica* *Lassioglosus sp*	**-Neutro semillas** **-Negativo visitas polinizadores**	**Rust, 1977**
	Bombus vagans *Archilochus colubris* *Bombus impatiens*	*Bombus affinis* *Appis mellifers* *Vespula maculifrons*	-Neutro **semillas y nectar**	**Zimmerman & Cook,**
Justicia aurea *(Selva Alta)*	*Phaethornis superciliosus* *Glaucis aenea* *Phaethornis longuemareus*	*Phaethornis longuemareus* Hormigas	**Negativo (experimental) semillas**	**McDade et al 1980**
Melanpyrum pratense		*Bombus terrestris* *Bombus lapidarius* *Apis mellifera*	**Positivo (polinizan)**	**Meidell, 1944**
Passiflora vitifolia	*Phaethornis superciliosus*	*Trigona sylvestrana* *Trigona fulviventris* Hormigas	**-Negativo nectar**	**Gill et al, 1982**
Pavonia dasypetala *(Selva Alta)*	*Phaethornis superciliosus*	*Trigona franki* *Trigona fulviventris* *Trigona sylvestrana* *Trigona corvina* *Trigona buyssoni* *Trigona ferricauda*	**Negativo (experimental) semillas polinizadores**	**Roubick 1988**
Pedicularis palustris	*Bombus hortum* *Bombus pascorum*	*Bombus lucorum* *Bombus terrestris*	**Positivo (polinizan)**	**Koeman-kwak 1973**

Tabla 5.1. Trabajos en donde se han reportado efectos de los ladrones de néctar sobre las plantas y sus polinizadores.

Especie	Polinizador	Robador	Efecto	Fuente
Penstemon kunthii	*Bombus muscorus* *Lampornis clemenciae* *Hylocharis leucotis* *Eugenes fulgens*	*Bombus jonelus* *Diglossa baritula* *Bombus pulcher* *Bombus trinomiatus*	Positivo (polinizan)	Lyon et al, 1971
Polemonium viscosum	*Delia sp.* *Bombus kirkbyellus* *Bombus sylvicola* *Halictidaee* *Andrenidae* *Hylex lineata*	*Formica neorufibarba*	-Negativo semillas	Galen, 1983
Trifolium pratense		*Bombus lucorum* *Apis mellifera*	Positivo (polinizan)	Hawkins, 1961
Tristerix longebracteanus		*Diglossa sp.*	Positivo (polinizan)	Graves,1982
Psittacanthus ramiflorus	*Amazilia beryllina* *Atthis heloisa* *Amazilia rutila* *Colibri thalassinus* *Eugenes fulgens* *Hylocharis leucotis* *Lampornis amethystinus* *Phaethornis superciliosus* *Selasphorus platycercus* *Selasphorus rufus*	*Diglossa baritula*	Positivo (transportan polen)	Este Estudio
Bytneria catalpifolia	*Hylocharis leucotis* *Lampornis amethistinus* Abejorros	*Diglossa baritula*	Positivo (transportan polen)	Este estudio
Calliandra grandifolia	*Amazilia beryllina* *Colibri thalassinus* *Eugenes fulgens* *Hylocharis leucotis* *Lampornis methysthinus* *Selasphorus rufus* *Selasphorus platycercus* *Tilmatura dupontii*	*Diglossa baritula*	Positivo (transportan polen)	Este estudio
Cirsium jaliscoense	*Amazilia beryllina* *Atthis heloisa* *Amazilia rutila* *Amazilia violiceps* *Eugenes fulgens* *Hylocharis leucotis* *Lampornis amethystinus* *Selasphorus platycercus*	*Diglossa baritula*	Positivo (transportan polen)	Este estudio
Salvia mexicana	*Amazilia beryllina* *Atthis heloisa* *Amazilia rutila* *Colibri thalassinus* *Eugenes fulgens* *Hylocharis leucotis*	*Diglossa baritula*	-Neutro semillas -Negativo concentracion nectar (experimental)	Este estudio

Tabla 5.1. Trabajos en donde se han reportado efectos de los ladrones de néctar sobre las plantas y sus polinizadores.

Especie	Polinizador	Robador	Efecto	Fuente
	Lampornis amethystinus *Stellula calliope* *Selasphorus platycercus* *Selasphorus rufus* *Amazilia violiceps* *Tilmatura dupontii*			
Salvia iodantha	*Amazilia beryllina* *Atthis heloisa* *Amazilia rutila* *Colibri thalassinus* *Eugenes fulgens* *Hylocharis leucotis* *Lampornis amethystinus* *Stellula calliope* *Selasphorus platycercus* *Selasphorus rufus* *Amazilia violiceps* *Tilmatura dupontii*	*Diglossa baritula*	-Neutro semillas	Este estudio
Fuchsia microphylla	*Amazilia beryllina* *Atthis heloisa* *Amazilia rutila* *Colibri thalassinus* *Eugenes fulgens* *Hylocharis leucotis* *Lampornis amethystinus* *Selasphorus platycercus* *Selasphorus rufus* *Tilmatura dupontii*	*Diglossa baritula*	-Neutro nectar -Neutro semillas si hay polinizacion (experimental)	Este estudio

la producción de néctar, algunos autores han encontrado, de manera experimental, que aquella se reduce en presencia de ladrones (Gill 1982, Mc Dade & Kinsman 1980, Norment 1988) y otros que no tienen efectos (Fritz 1981, Zimmerman & Cook 1985). El efecto de las aves que actúan como ladrones de néctar sobre la producción de semillas no se conoce, y no existe ningún trabajo de índole experimental al respecto. El presente estudio constituye el primer trabajo experimental realizado con aves ladronas de néctar bajo condiciones naturales. Sus resultados muestran la factibilidad del enfoque asi como su relevancia en el entendimiento de procesos como la polinización biótica.

El estudio integral de las interacciones planta-polinizador-ladrón en un tiempo relativamente largo como el que se realizó en esta tesis, muestra una alta diversidad en cuanto a las especies interactuantes, siendo este uno de los sistemas más complejos que se ha estudiado, comparable solamente con el descrito por Stiles (1980a) en una selva húmeda en Costa Rica, nueve grados de latitud más cerca del Ecuador. La alta diversidad que se presenta en Manantlán refleja por un lado la indudable riqueza florística y faunística de la zona, pero puede ser también un reflejo de lo parcialmente estudiados que están los sistemas de polinización biótica.

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