Hummingbirds and Their Floral Resources in a Tropical Dry Forest in Mexico

Ma. del Coro Arizmendi; Juan Francisco Ornelas

Biotropica, Vol. 22, No. 2. (Jun., 1990), pp. 172-180.

Stable URL:
http://links.jstor.org/sici?sici=0006-3606%28199006%2922%3A2%3C172%3AHATFRI%3E2.0.CO%3B2-W

Biotropica is currently published by The Association for Tropical Biology and Conservation.

BIOTROPICA 22(2): 172–180 1990

Hummingbirds and Their Floral Resources in a Tropical Dry Forest in Mexico[1]

Ma. del Coro Arizmendi

Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70–275
Ciudad Universitaria, Coyoacan 04510, México, D.F., México

and

Juan Francisco Ornelas

Department of Ecology and Evolutionary Biology, The University of Arizona, Tucson, Arizona 85721, U.S.A.

ABSTRACT

We studied temporal and spatial relationships among hummingbirds and their food flowers in a tropical dry forest on the western coast of México. From June 1985 to July 1986 we recorded flowering phenology, nectar production, and hummingbird visits to flowers, and made morphological measurements of hummingbirds and plants. Twenty-three species of plants were studied, and ten of them were pollinated exclusively by hummingbirds. Out of the six hummingbird species we found, only two were permanent residents (*Amazilia rutila* and *Cynanthus latirostris*), two were altitudinal wanderers (*Chlorostilbon canivetii* and *Heliomaster constantii*), and two were winter visitors (*Archilochus colubris* and *A. alexandri*). The most abundant resident was *A. rutila*. It used clumped flowers and defended feeding territories around them. The other species in the area, subordinates to *A. rutila*, used less plentiful resources without the establishment of territories.

RESUMEN

Se estudiaron las relaciones temporales y espaciales entre los colibríes y sus flores en una Selva Baja Caducifolia en la costa oeste de México. Registramos durante un año (1985–1986), la floración, producción de néctar, tasas de forrajeo asi como todos los datos merísticos tanto de las plantas como de los colibríes. La comunidad de aves nectarívoras esta formada basicamente por 6 especies de colibríes que utilizan a 23 especies de plantas a lo largo del año. Diez de estas son exclusivamente polinizadas por colibríes. Solo dos especies de colibriés son residentes (*Amazilia rutila* y *Cynanthus latirostris*), dos realizan movimientos estacionales (*Chlorostilbon canivetii* y *Heliomaster constantii*) y dos son visitantes de invierno (*Archilochus colubris* y *A. alexandri*). *A. rutila* es la especie residente más abundante y jerárquicamente la dominante. Esta especie monopoliza los recursos, estableciendo territorios en los lugares con mayor abundancia y disponibilidad de éstos. Las demás especies utilizan recursos más escasos mediante forrajeo no territorial.

THE ORGANIZATION OF HUMMINGBIRD communities has been studied intensively in the past 15 years, especially in the moist forest (Stiles 1981). Feinsinger (1976, 1978) and Feinsinger and Colwell (1978) proposed that these communities are structured partly by a dominance hierarchy among species which affects access to nectar resources.

Studies about the ecology of hummingbirds in tropical dry forests are less common. The impact of seasonal flowering on the biology of the hummingbirds was studied by Wolf (1970); the territoriality at a tropical flowering tree was analyzed by Stiles and Wolf (1970); while Heithaus (1974) studied the community organization among plants and their pollinators.

The ecology of Mexican hummingbirds has not been intensively studied despite the country's fauna of 54 species (Ornelas 1987; AOU 1983), which occupy varied topography and vegetation in seasonal environments. Previous work has focused largely on visitation to specific plants (Eguiarte & del Río 1987; Martínez del Río & Eguiarte 1987; Toledo 1974, 1975). Only few studies concern community organization (Des Granges 1979, Eguiarte & del Río 1987, Lyon 1976). This work is the first year-round study in a tropical dry forest in México.

STUDY AREA

Field work was conducted between June 1985 and July 1986 at the Estación de Biología "Chamela" on the Pacific Coast of Jalisco (19°30'N and 105°03'W). The station reserve includes about 1600

[1] Received 14 January 1988, second revision accepted 10 March 1989.

ha of land, between 30 m and 500 m elevation. The climate is dominated by strongly seasonal rainfall. Mean annual rainfall is 748 mm (Bullock, 1986 and pers. comm.) with a long dry season extending from November into June (Bullock 1986), and the mean annual temperature is 24.9°C (1977–1984; Bullock 1986). The sites contain tropical dry deciduous forest with some patches of tropical semideciduous forest in the arroyos (Lott 1985). Details on the structure and composition of the vegetation are given by Lott *et al.* (1987).

METHODS

We determined flowering phenology for each species by conducting monthly censuses along permanent transects. Floral morphology and nectar production were measured for the most abundant hummingbird visited species. For each species we measured the length and width of corolla and the length of calix. For 12 species we also determined the rates of nectar secretion in flowers enclosed in mosquito net bags. Nectar concentration was measured as the equivalent percent sucrose (weight/total solution weight) with a pocket refractometer (ERMA mod. 101190–32) and converted to mg of sucrose (Bolten *et al.* 1979). For these measurements, between 60 and 80 buds were bagged in the evening and nectar accumulated in about ten flowers was measured every two hours from dawn to dusk on the following day. We used one to four individual plants per species.

Hummingbird censuses were conducted monthly along permanent transects (two km long and 100 m wide), following Emlen's method (Emlen 1971, 1977). Two transects were located inside the station, one mainly in deciduous forest (El Tejón, A) and the second (Eje Central, B) almost parallel to the dry bed of an arroyo and intersecting several patches of semideciduous forest. The third transect was located in a disturbed area near the station (La Virgencita, C). For all birds counted we determined their position in four vegetation strata: lower understory, middle understory, subcanopy, and canopy.

We captured hummingbirds with mist nets to measure exposed culmen, length of wing, total length, wing cord, and weight. We also recorded any evidence of reproduction, fat, and molt.

To estimate the use of flowers by different species, we observed 23 plant species and recorded all hummingbird visits to them. For each visit we recorded total observation time, time of the visit, foraging methods utilized by the bird (sitting or hovering), territorial defense, aggressive interactions and their results, visit height, plant height, and foraging method. In this last case, foraging time was defined as the total time spent by the bird feeding on flowers. We measured flower conspicuousness to human observers with an ordinal scale (1 = very conspicuous; 2 = moderately conspicuous; 3 = inconspicuous).

Most observations were performed during the morning (07:00–11:00 am) and from late afternoon to dusk (16:30–19:30 pm). However, in some plants we made observations all day long, at the same time as the nectar measurements.

RESULTS

THE PLANTS.—We observed hummingbird visits to a total of 23 plant species (Table 1) mainly epiphytes, vines, and herbs. The overall flowering peak occurred in June, at the end of the dry season, when we found 10 species in flower. Only one species (*Ipomoea wolcottiana*) bloomed in December (see Bullock *et al.* 1987).

Hummingbirds used flowers in all levels of the forest, but predominately the medium to high levels. In the entomophilous tree, *Vitex mollis,* birds visited only the lower part of the crown; the higher parts were used by territorial bees (Table 1).

Most flowers were conspicuous to the human eye (Table 1), contrasting with the background foliage, except for the bee-pollinated *Vitex mollis,* where odor seemed to be the principal attractant (Table 1). All flowers investigated last only one day. The lengths of corollas ranged from 10.6–74.0 mm among species; the modal corolla length was between 30 and 40 mm (Table 2). Two species had corollas longer than 50 mm, *Nopalea karwinskiana* was defended during its blooming peak by *Heliomaster constantii* while *Amazilia rutila* visited earlier in the season before the arrival of *H. constantii* to the study area. *Erythrina lanata* was visited only by *H. constantii,* the largest of all the hummingbirds at the site.

Among the 12 plant species examined, nectar production ranged from 0.74 to 26.9 μl/flower/day (Table 2). Sugar concentration varied from 12.7 to 29.9 percent (Table 2) and for ornithophilous flowers from 18.1 to 29.1 percent. The amount of nectar produced (mg of sugars) is relatively low (range 0.2–8.8).

The flowers were divided into three corolla sizes, short (10–20 mm), medium (25–50 mm) and long (65–75 mm) (Table 2). Among species pollinated exclusively by hummingbirds we found a positive correlation (Spearman correlation) between the corolla length and the total amount of nectar produced

TABLE 1. *Morphological features of flowers visited by hummingbirds at Chamela, Jalisco.*

Plant species	Biological form	Pollinator[a]	Blooming peak	Visitors[b]	Flower type	Color	Arrange-ment	Flower cons.	Spatial segregation
Nopalea karwinskiana	Tree	Hum.	Feb–June	Ar-Hc	Tube	Pink	Solitary	1	Crown
Tillandsia bartramii	Epiphyte	Hum.	May	Ar	Tube	Purple	Solitary	2	Crown
Tillandsia paucifolia	Epiphyte	Hum.	Mar–June	Ar-Hc-Cc	Tube	Purple	Inflo	2	Crown-Down
Tillandsia dasyrifolia	Epiphyte	Hum.	May	Ar	Tube	Red	Inflo	2	Crown
Clytostoma binatum	Vine	Hum.	June	Ar	Tube	Pink	Solitary	2	Crown
Ipomoea bracteata	Vine	Hum.	Jan–Mar	Ar-Cl	Tube	Purple	Inflo	1	Crown-Down
Justicia mexicana	Herb	Hum.	Oct–Nov	Ar-Cc-Cl	Tube	Red	Inflo	1	Crown
Erythrina lanata	Tree	Hum.	Jan–May	Hc	Tube	Purple	Inflo	2	Crown
Hamelia versicolor	Herb	Hum.	June–Nov	Ar-Cc-Hc-Cl	Tube	Red	Inflo	1	Crown-Int.
Opuntia excelsa	Tree	Hum.	June–July	Ar-Hc	Cup	Yellow	Solitary	1	Crown
Mirabilis sp.	Herb	Hum.	Sept	Cl-Cc	Tube	Purple	Solitary	2	Crown-Int.
Ceiba aesculifolia	Tree	Hum-Bat	May–June	Ar-Hc-Cl	Cup	White	Solitary	1	Crown-Int.
Cordia seleriana	Vine	Hum-Insect	Apr–June	Cc	Tube	White	Inflo	1	Crown
Combretum farinosum	Vine	Hum-Per	Jan–Apr	Cc-Ar-Cl	Cup	Orange	Inflo	1	Crown-Down
Ipomoea quamoclit	Vine	Hum-Insect	Sept–Nov	Ar	Tube	Red	Solitary	1	Crown-Down
Ipomoea wolcottiana	Tree	Insect	Dec–Apr	Ar-Cc-Cl	Tube	White	Solitary	1	Crown-Int.
Vitex mollis	Tree	Insect	May–June	Cc-Cl-Ar	Tube	Purple	Inflo	3	Down
Tabebuia donell-smithii	Tree	Insect	June–July	Hc	Tube	Yellow	Inflo	1	Crown
Tabebuia rosea	Tree	Insect	June	Ar-Cl	Tube	Pink	Inflo	1	Crown
Croton suberosus	Herb	Insect	Aug–Sept	Cc	Cup	White	Inflo	3	Crown-Int.
Serjania sp.	Herb	Insect	Sept	Cc	Cup	—	Solitary	3	Crown-Int.
Caesalpinia pulcherrima	Tree	Insect	Sept–Oct	Ar-Cc-Cl	Cup	Orange	Inflo	1	Crown
Pithecellobium mangens	Tree	Insect	May–June	Cl	Brush	White	Inflo	2	Crown

[a] Hum = Hummingbird; Per = Perching bird.
[b] Ar = *Amazilia rutila*; Hc = *Heliomaster constantii*; Cl = *Cynanthus latirostris*; Cc = *Chlorostilbon canivetii*.

TABLE 2. *Mean length of the corolla, amount and quality of nectar produced by plants visited by hummingbirds at Chamela, Jalisco.*

Plant species	Number flowers measured	Corolla length (mm)	Nectar[1] volume (μl)	Nectar concentration (%)	mg of sugar
Croton suberosus	50	8.0 ± 0.1	—	—	—
Vitex mollis	95	10.1 ± 0.2	0.9 ± 0.4	25.7 ± 0.3	0.27
Combretum farinosum	95	10.6 ± 0.5	20.3 ± 8.6	12.7 ± 2.3	2.73
Cordia seleriana	20	12.4 ± 0.8	26.5	—	1.11
Mirabilis sp.	50	14.2 ± 1.1	0.7 ± 0.3	21.8 ± 12.5	0.17
Hamelia versicolor	275	16.9 ± 2.3	8.6 ± 4.5	18.1 ± 5.3	1.68
Clytostoma binatum	100	27.2 ± 3.2	—	—	—
Ceiba aesculifolia	40	29.9 ± 1.3	—	—	—
Justicia mexicana	99	33.7 ± 3.9	5.0 ± 2.6	26.9 ± 4.6	1.51
Ipomoea bracteata	100	35.3 ± 5.7	16.1 ± 4.5	28.9 ± 1.7	5.27
Tillandsia paucifolia	26	39.0 ± 3.9	0.7 ± 0.7	26.7	0.22
Ipomoea wolcottiana	40	42.1 ± 5.5	29.6 ± 13.9	+32	—
Opuntia excelsa	25	49.8 ± 3.7	8.1 ± 8.4	24.3 ± 2.7	2.17
Nopalea karwinskiana	32	69.4 ± 6.6	23.1 ± 6.1	27.3 ± 2.3	7.06
Erythrina lanata	31	73.9 ± 9.2	26.9 ± 8.8	29.1 ± 1.4	8.86

[1] Mean volume per flower per hour.

($r = 0.68$; $P < 0.05$) (Fig. 1). Flowers pollinated by hummingbirds were medium to long tubed size, except for the short-tubed *Hamelia versicolor.*

Territorial hummingbirds visited flowers throughout the day. Trapliners were most active at dawn and dusk.

THE HUMMINGBIRDS.—The hummingbird fauna at Chamela was largely transient, with only two resident species, *Amazilia rutila* and *Cynanthus latirostris,* and two seasonal wanderers, *Heliomaster constantii* and *Chlorostilbon canivetii.* Two more species appeared during long distance migration, *Archilochus colubris* and *A. alexandri.* Also *Amazilia violiceps* was recorded after a hurricane in October 1986 (Ornelas, pers. comm.). *Phaethornis superciliosus* was registered visiting introduced plants in the gardens around the station buildings (Martínez del Río and Ornelas, pers. comm.) in June 1988. Both are considered occasional visitors and for that reason are not discussed further.

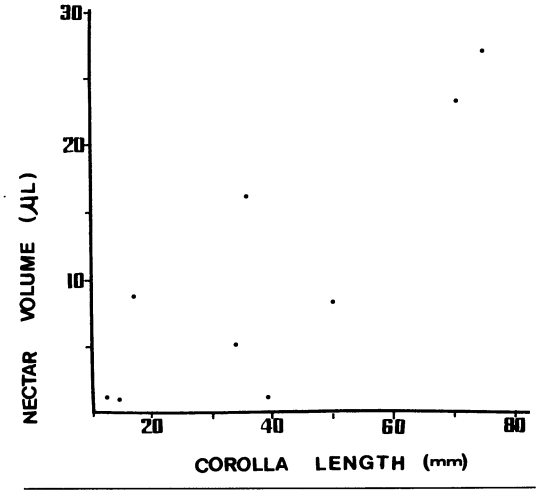

FIGURE 1. Relation between corolla length and volume of nectar produced by plants pollinated by hummingbirds at Chamela, Jalisco (Spearman correlation, $r = 0.68$; $P < 0.05$).

The seasonal abundance of the two residents and the two wanderer species, determined during censuses of the entire bird community (Arizmendi *et al.* 1987), is shown in Figure 2. Relative densities for the long distance migratories are not available because of their short permanence in the zone. The relative densities were calculated using Emlen's method (1971, 1977).

The most abundant hummingbird at Chamela was *Amazilia rutila* (Fig. 2). Its relative abundance changes seasonally in the three transects, with the changes in the abundance and location of flowers. *A. rutila* was usually most abundant at "Eje Central," where the predominant vegetation is tropical semideciduous forest. It nested in the tropical deciduous forest from July to September (Arizmendi & Ornelas, pers. comm.).

The other resident at Chamela was *Cynanthus latirostris,* slightly smaller in body size than *A. rutila* (Table 3). Less abundant than *A. rutila,* it

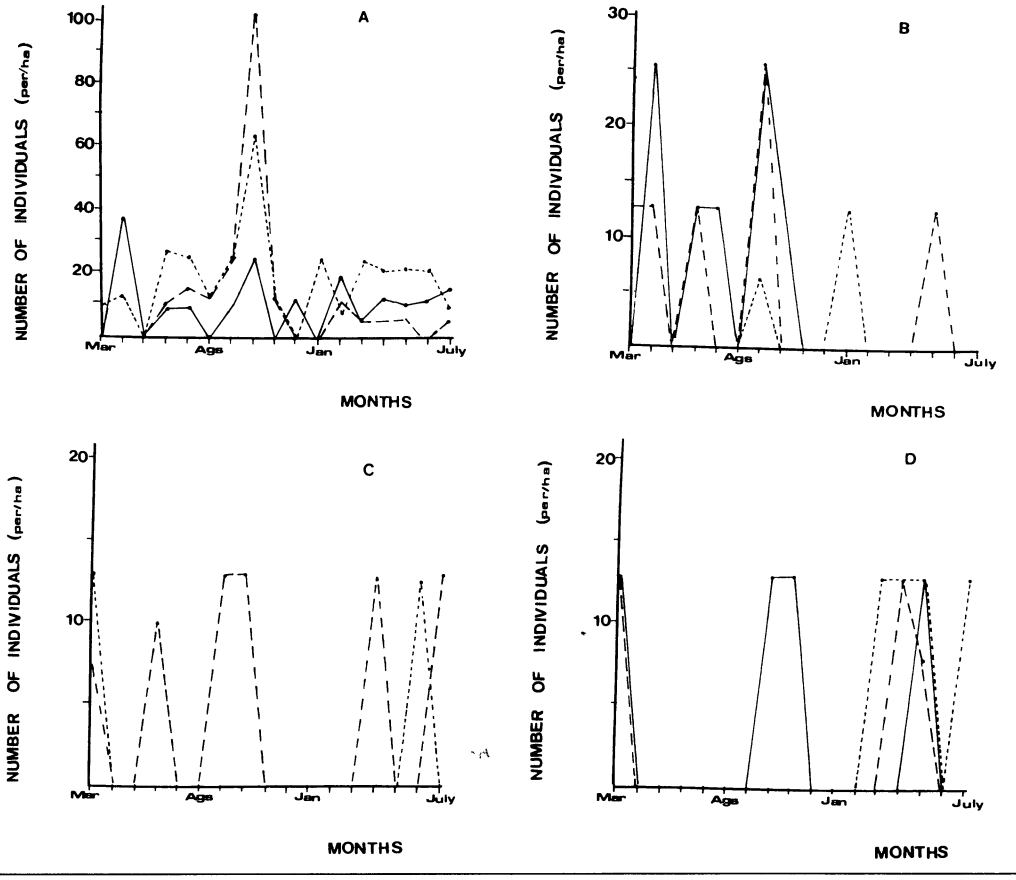

FIGURE 2. Densities of the hummingbirds of Chamela, Jalisco. A) *Amazilia rutila*; B) *Heliomaster constantii*; C) *Chlorostilbon canivetii*; D) *Cynanthus latirostris* – – – EJE CENTRAL, ····· TEJON, ——LA VIRGENCITA.

occurred in the three transects, but moved between places with abundant resources.

The largest hummingbird at Chamela, (*H. constantii*), moved among habitats to follow flowering seasons. It nested in the Chamela area from January to February (Ornelas, pers. comm.), and was most abundant in the dry season and in the disturbed site (C) (Fig. 2). It fed almost throughout the year on aerial arthropods.

The smallest hummingbird of the area (*C. canivetii*) was also a wanderer. It was most abundant in the dry season and at the beginning of the rainy season. It fed from several entomophilous flowers, and was generally excluded from ornithophilous

TABLE 3. *Morphological measurements of the hummingbirds of Chamela, Jalisco. Data from birds captured in the zone and from skins in the Bird Collection of the Instituto de Biología, Universidad Nacional Autónoma de México.*

Bird species	Weight (g)	Exposed culmen (mm)	Wing disc load	Period of molt	Presence of fat	Reproduction
Amazilia rutila	4.3 ± 0.1	22.6 ± 1.3	0.0379	Jan–May	Nov–Jan	Jan–Apr
Cynanthus latirostris	2.9 ± 0.3	20.0 ± 0.4	0.0259	May–Sept	May	Sept
Chlorostilbon canivetii	2.1 ± 0.3	13.6 ± 1.4	0.0247	Nov–May	July–Nov	—
Heliomaster constantii	7.5 ± 0.9	33.7 ± 1.2	0.0441	May	Sept–Nov	Feb
Archilochus colubris	2.8 ± 0.3	16.5 ± 1.1	0.0343	Feb–May	Sept–May	—

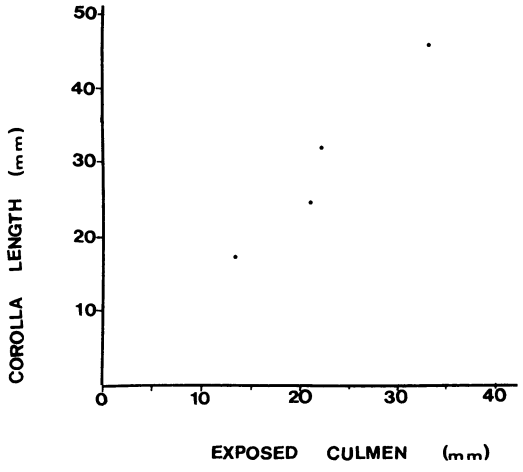

FIGURE 3. Relation between hummingbird's bill and corolla length of the plants visited by hummingbirds at Chamela, Jalisco (Pearson correlation, $r = 0.986$; $P \ll 0.05$).

flowers by the larger species or even by bees (*Xylocopa* sp). It was never detected in the disturbed site (Fig. 2).

Hummingbirds in Chamela can be divided in two bill-size groups: *Heliomaster constantii* and *Amazilia rutila,* had bills of more than 22 mm long; the other four, *C. latirostris, A. colubris, A. alexandri,* and *C. canivetii* had bills of less than 20 mm (Table 3). We found a positive correlation (Pearson correlation) between mean hummingbird's bill length and mean corolla length of the flowers visited by each bird species ($r = 0.9863$; $P \ll 0.05$) (Fig. 3).

Vertical stratification of hummingbirds was measured as the number of individuals of each species noted in each of the four strata defined. Most hummingbirds occurred in the higher strata (Table 4).

A. rutila was territorial and the dominant species (Table 5), won 92 percent of the interspecific encounters chased. The other year-round resident, *Cynanthus latirostris,* won only 2.6 percent of the interspecific encounters. The transient, *H. constantii,* was only able to win encounters with *A. rutila.* During its seasonal residence at the deciduous forest, *H. constantii* was territorial, defending resources such as *Nopalea karwinskiana.* Its relative success against *A. rutila* on *Nopalea karwinskiana* may have resulted from its more efficient exploitation of long-tubed flowers.

A. colubris and *A. alexandri* acted as trapliners during their short residence in the area, obtaining their nectar from patches not defended by the residents. However, in some cases *A. colubris* defended territories at *Justicia mexicana* when flowers were very abundant (F. G. Stiles, pers. comm.).

TABLE 4. *Stratification of the hummingbirds in the vegetation of Chamela, Jalisco.*

Bird species	Lower understory	Middle understory	Subcanopy	Canopy
Amazilia rutila	21	60	103	18
Cynanthus latirostris	0	5	11	6
Chlorostilbon canivetii	1	10	11	4
Heliomaster constantii	1	4	11	4

Small-billed species visited only short to medium sized flowers, whereas long-billed species visited only long-tubed flowers. *A. rutila,* a medium to long-billed species, visited almost all flowers (Table 6).

DISCUSSION

ORGANIZATION OF THE HUMMINGBIRD COMMUNITY.—Organization among nectarivorous birds was very similar to that reported by Feinsinger (1976) at Monteverde, Costa Rica. The most abundant resident, *Amazilia rutila,* was a core species, monopolizing clumped resources and forcing other species to obtain their food elsewhere. Despite its size, *Heliomaster constantii* rarely dominated *A. rutila.* It is a very insectivorous bird depending on nectar only when floral resources are abundant (Des Granges 1979). *Cynanthus latirostris,* the other resident was always subordinated to *Amazilia rutila,* using resources not used by the dominant. *Chlorostilbon canivetii,* the smallest species, restricted its stay at Chamela to those months when the abundance of entomophilous flowers was greatest. The low abundance of the winter visitors, *Archilochus colubris* and *A. alexandri,* may result from competition with other species for the scarce resources present during winter.

Body size is an important factor in dominance systems (Eguiarte and del Río 1987, Martinez del Río and Eguiarte 1987). Larger hummingbirds have high energetic requirements, so the predominant strategy in the dry forests is to move in search of rich resources among habitats (Des Granges 1979).

TABLE 5. *Aggressive encounters registered with an absolute winner.*

	Loser				% Intra-specific encounters	% Inter-specific encounters	% Inter-specific encounters won
	Ar	Hc	Cl	Cc			
Winner							
Ar	35	36	35	26	25	75	92
Hc	8	6	2	0	12	88	21.7
Cl	0	0	8	1	18	82	2.6
Cc	0	0	0	5	16	84	0

Total encounters registered = 212.

Smaller hummingbirds are unable to chase the bigger ones and are forced to obtain their food through non-territorial foraging. Medium sized birds are the most abundant residents. These are usually aggressive dominants that defend territories to obtain nectar consistently.

The nectarivorous bird guild responds readily to changes in nectar abundance. In general, residents have high year long abundances, forming the core of the guild to which, depending on the seasonal availability of food, additional species are added (Des Granges 1979). Residents feed preferentially on tubular flowers and defend feeding territories around them. Tropical wanderers are high reward trapliners and have a high status of dominance (Des Granges 1979). Migrants are small birds and thus tend to be subordinates to residents and wanderers (Des Granges 1979).

The presence of both territorial and traplining species is an important aspect of the high diversity of tropical nectarivorous bird guilds. The existence of these complementary strategies results in the sta-

TABLE 6. *Hummingbird visits to the different plant species. (In order of corolla length Top = shortest, bottom = longest; and for birds in order of bill length from the shortest (Left) to the longest (Right)).*

Plant species	Hummingbird species					Total # of flowers visited	Total observa. time
	Cc	Ac	Cl	Ar	Hc		
Pithecellobium mangens	104	0	0	0	0	104	2
Caesalpinia pulcherrima	0	0	0	243	0	243	3
Croton suberosus	R[1]	0	0	58	0	58	3
Vitex mollis	1847	0	0	52	0	1899	17.5
Combretum farinosum	134	0	230	687	0	1051	40
Cordia seleriana	130	0	0	55	0	165	9.5
Mirabilis sp.	0	0	627	0	0	627	2
Hamelia versicolor	592	0	324	1056	41	2013	46
Clytostoma binatum	0	0	0	R	0	—	—
Ceiba aesculifolia	0	0	25	169	107	301	6.5
Ipomoea quamoclit	2	0	1	2	0	5	3
Justicia mexicana	0	0	32	14	0	46	4
Ipomoea bracteata	0	12	124	525	34	695	16.5
Opuntia excelsa	2	0	0	371	46	419	3.5
Tillandsia paucifolia	0	0	8	90	1	99	9.5
Tillandsia dasyrifolia	0	0	0	85	0	85	4.5
Tillandsia bartramii	0	0	0	119	0	119	7
Psittacanthus calyculatus	0	99	0	39	0	138	†[2]
Ipomoea wolcottiana	0	148	281	46	0	475	17
Nopalea karwinskiana	0	0	0	57	321	378	29
Erythrina lanata	0	0	0	0	5	5	8
Tabebuia rosea	0	0	0	R	R	—	—
Tabebuia donnell-smithii	0	0	0	0	3	3	2

[1] Visit registered but not counted.
[2] F. G. Stiles (pers. comm.).

ble coexistence of closely similar species (Des Granges 1979).

ORGANIZATION OF THE PLANT COMMUNITY.—Ten of the plants we examined are likely to be pollinated by hummingbirds, five by hummingbirds in combination with another animal, and eight are pollinated by insects, with hummingbirds acting only as nectar thieves (Table 1).

All flowers presumably pollinated by hummingbirds exhibit the ornithophilous syndrome (defined by Faegri & van der Pijl 1979; Stiles 1976, 1978, 1981) such as red or reddish tubular corolla, absence of odor, and absence of a platform.

The amount and concentration of nectar is a function not only of the reproductive strategy of the plant, but also of the availability of water, sunlight and nutrients in soil (Baker 1978) and the general environment (Corbet 1978, Corbet *et al.* 1979, Búrquez 1988). In Chamela the amount and concentration of nectar of flowers pollinated by birds corresponds with that reported by Baker (1978) for ornithophilous flowers.

Janzen (1967) states that many tree species in lowland Central America have evolved the timing of their flowering and fruiting with the dry season. The primary advantage of the dry season is the lack of interference of the flowering with vegetative process and the maximization of the use of pollinators and dispersal agents. In Chamela the hummingbird visited plants flowered in the dry season, consistent with the hypothesis of Janzen (1967).

HUMMINGBIRD-FLOWER ASSOCIATIONS.—The association between hummingbirds and their flowers is affected by flower morphology (length and shape of corolla) (Stiles 1976, 1981). Long-billed hummingbirds that visit long-tubed flowers obtain richer rewards than smaller species (Fig. 1 and 3). Short-billed hummingbirds can extract nectar efficiently only from short-tubed flowers. *C. latirostris* visits those flowers under 30 mm in length. *A. rutila* visits all plant species except *Erythrina lanata* which has the longest corolla of all the flowers. *H. constantii,* the largest hummingbird of the zone, only visits medium to long-tubed flowers with rich rewards. Only in *Erythrina lanata* flower piercing was observed. However, the flower piercer was never identified, but it is likely to be an early morning foraging bee (Heithaus, pers. comm.).

The relationship between hummingbirds and their flowers in Chamela is not species-specific, both parts being generalists. Hummingbirds change food choices as resources change. In addition birds are very mobile, moving from place to place in search of high abundance of resources.

Acknowledgments

We are grateful to S. H. Bullock, F. G. Stiles, L. Eguiarte, C. Martinez del Río, A. Búrquez, E. R. Heithaus, P. Feinsinger and D. S. Dobkin whose comments and criticisms improved the manuscript. To L. Navarijo, Curator of the Bird Collection of the Instituto de Biología, Universidad Nacional Autónoma de México for the facilities given. H. Berlanga, L. Márquez-Valdelamar, and A. M. Chávez-López enthusiastically collaborated in the field. Plants were determinated by A. Solís-Magallanes and E. Lott. The station personnel gave logistic support. M. C. Arizmendi was supported by scholarship 48277 of the CONACyT. PROAVIS, A. C. provided financial support.

LITERATURE CITED

AMERICAN ORNITHOLOGIST'S UNION (AOU). 1983. Checklist of North American Birds. American Ornithologist's Union. 877 pp.

ARIZMENDI, M. C., H. BERLANGA, L. MARQUEZ-VALDELAMAR, L. NAVARIJO, Y F. ORNELAS. Análisis de la avifauna de la región de Chamela, Jalisco. Análes del Instituto de Biología, Universidad Nacional Autónoma de México. In press.

BAKER, H. C. 1978. Chemical aspects of the pollination biology of woody plants in tropics. *In* P. B. Tomlinson and M. H. Zimmermann (Eds.). Tropical trees as living systems. Cambridge University Press.

BOLTEN, A. B., P. FEINSINGER, H. G. BAKER, AND I. BAKER. 1979. On the calculation of sugar concentration in flower nectar. Oecologia 41: 301–304.

BULLOCK, S. H. 1986. Climate of Chamela Jalisco and trends in the south coastal region of México. Arch. Met. Geoph. Brod. Ser. B 36: 297–316.

———, R. AYALA, I. BAKER, AND H. G. BAKER. 1987. Reproductive biology of the tree *Ipomoea wolcottiana* (Convolvulaceae). Madroño 34(4).

BÚRQUEZ, J. A. 1988. Studies on nectar secretion. Ph.D. Dissertation, University of Cambridge.

CORBET, S. A. 1978. Bees and the nectar of *Echison vulgare. In* A. J. Richards (Ed.). The pollination of flowers by insects. Linnean Society Symposium Series 6. Academic Press. London.

CORBET, S. A., P. G. WILLMER, W. L. BEARMENT, AND D. M. UNWIN. 1979. Post-secretion determinants of sugar concentration in nectar. Plant, Cell Environ. 2: 293–308.

DES GRANGES, J. L. 1979. Organization of a tropical nectar feeding bird guild in a variable environment. The Living Bird. Seventeenth Annual. Cornell Laboratory of Ornithology 199–236.
EGUIARTE, L., Y C. MARTÍNEZ DEL RÍO. 1987. El néctar y el polen como recursos: el papel ecológico de los visitantes a las flores de *Pseudobombax ellipticum* (H.B.K.) Dugand. Biotropica 19(1): 74–82.
EMLEN, J. T. 1971. Population densities derived from transect counts. The Auk 88: 323–342.
———. 1977. Estimating breeding season bird densities from transect counts. The Auk 95(3): 455–468.
FAEGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination biology. Second Revised Edition. Pergamon Press, Oxford England.
FEINSINGER, P. 1976. The organization of a tropical guild of nectarivorous birds. Ecol. Monogr. 46: 257–291.
———. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. Ecol. Monogr. 48: 269–287.
———, AND R. K. COLWELL. 1978. Community organization among neotropical nectar-feeding birds. Am. Zool. 18: 779–795.
HEITHAUS, E. R. 1974. The role of plant-pollinator interactions in determining community structure. Ann. Mo. Bot. Gard. 61(3): 675–691.
JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21: 620–637.
LOTT, E. J. 1985. Listados Florísticos de México III. La Estación de Biología Chamela, Jalisco. Instituto de Biología, U.N.A.M. 47 pp.
———, S. BULLOCK, AND A. SOLIS-MAGALLANES. 1987. Floristic diversity and structure of upland and arroyo forest in Costal Jalisco. Biotropica 19(2). In press.
LYON, D. L. 1976. A montane hummingbird territorial system in Oaxaca, México. Wilson Bull. 88(2): 280–299.
MARTÍNEZ DEL RÍO, C. AND L. EGUIARTE. 1987. Bird visitation to *Agave salmiana:* comparisons among hummingbirds and perching birds. Condor 89: 357–363.
ORNELAS, J. F. 1987. Rediscovery of the Rufous-Crested Coquette (*Lophornis delatreii brachylopha*) in Guerrero, México. Wilson Bull. 99: 719–721.
STILES, F. G. 1976. Taste preferences and flower choice in hummingbirds. Condor 78(1): 10–26.
———. 1978. Ecological and evolutionary implications of hummingbird pollination. Am. Zool. 18: 715–727.
———. 1981. Geographical aspects of bird-flower coevolution with particular reference to Central America. Ann. Mo. Bot. Gard. 68: 323–351.
———, AND L. L. WOLF. 1970. Hummingbird territoriality at a tropical flowering tree. Auk 87: 467–491.
TOLEDO, V. M. 1974. Observations on the relationship between hummingbirds and *Erythrina* spp. Lloydia 37: 482–487.
———. 1975. La Estacionalidad de las Flores Utilizadas por Colibríes de una selva húmeda en México. Biotropica 7(1): 63–70.
WOLF, L. L. 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. Condor 72: 1–14.