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SEASONAL PATTERNS AND COEVOLUTION IN THE HUMMINGBIRD-FLOWER COMMUNITY OF A COSTA RICAN SUBTROPICAL FOREST

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ABSTRACT. This two-year study seeks to quantify the relations of the breeding, molt, and population movements of hummingbirds, with the flowering seasons of their foodplants, at La Montura, a site in premontane rain forest at 1000 m on the Caribbean slope of Costa Rica. The community comprises 22 hummingbird species (9–10 residents, 5–6 regular seasonal visitors, the rest rare to accidental), that collectively visit at least 70 species of plants, ca. 50 of which they pollinate.

Patterns of flower visitation by the birds allow partitioning of the community into subcommunities, each with its own seasonal rhythm. These are: (a) Lancebill Subcommunity: the Green-fronted Lancebill (*Doryfera ludovicae*) and five species of large shrubby epiphytes, and probably several bromeliads. Morphologically, the bird's long, slender, nearly straight bill and the flowers' correspondingly shaped corolla tubes characterize this subcommunity. The five principal foodplants bloomed in a nearly perfectly staggered sequence through the study period; breeding in *D. ludovicae* coincided with periods of greatest flower abundance, molt with intermediate flower availability. (b) Hermit Subcommunity: chiefly the Green Hermit (*Phaethornis guy*) with its long, decurved bill, and 19 understory and subcanopy flowers with correspondingly shaped corollas. Flower availability is high during breeding, peaks during the period of molt-breeding overlap, and declines during molt and quiescent periods; the species of *Heliconia* appear to supply critical nectar resources for breeding. *P. guy*'s foodplants show staggered blooming sequences when the bird's breeding and nonbreeding periods are analyzed separately. Also included here is the White-tipped Sicklebill (*Eutoxeres aquila*), whose visits to the study area are linked to the blooming of a single foodplant. (c) *Heliodoxa-Marcgravia* Subcommunity: the Green-fronted Brilliant (*Heliodoxa jacula*) and three species of sphingid- or bat-pollinated *Marcgravia*, about which the bird's breeding and molting cycles appear to be organized. The three *Marcgravia* species bloom in a staggered sequence that is exploited by *H. jacula*, but this cannot reflect a coevolutionary relationship as the hummingbird is a nectar thief. (d) "Generalized" Subcommunity: various small- to medium-sized, straight-billed hummingbirds, and flowers with straight, short- to medium-length corollas. Sufficient overlap in flower visitation exists within this assemblage to preclude further subdivision. The principal hummingbird species (*Lampornis hemileucus*, *Eupherusa nigriventris*, *Elvira cupreiceps*) breed in close association with the blooming of a series of canopy epiphytes, mostly in the family Ericaceae. Many individuals of the latter two species, plus *Colibri delphinae*, emigrate following breeding and at least the start of molt; their places are taken by several species of post-breeding seasonal visitors from other elevations, which mostly exploit the flowers of the abundant understory treelet *Cephaelis elata*.

Most La Montura hummingbirds breed from the mid- to late wet season, through the early dry season, roughly October through March, and molt from March through June, into the early rainy season. Males of many species molt one to two months ahead of females. The cycle of *H. jacula* is displaced one to two months earlier than those of most species, while that of *P. guy* is nearly the opposite: breeding April–September, molting July–November. Differences in seasonality in other hummingbird-flower communities reflect different climatic regimes and taxonomic affinities—e.g., in all areas Ericaceae bloom mainly in the wet season, *Heliconia* mostly June–August.

The various hummingbird-flower communities in the wet forests of Costa Rica show similar divisions into subcommunities, given different species richnesses and taxonomic affinities. In dry forest and second growth, most or all species pertain to the generalized subcommunity. The relation between plant-pollinator interactions and flowering seasons is reassessed in the light of changing nectar demands of the birds due to breeding and molt. It is concluded that competition for pollinators may be an important selective force in the spacing of flowering seasons, but that its intensity varies according to the annual cycles of the pollinators, and cannot be assessed properly without taking the pollinators' biology into account. Finally, based on eco-

logical and biogeographical evidence, it is argued that many (but by no means all) of the bird-flower interactions in the La Montura community represent true coevolved mutualisms.

RESUMEN. Este estudio de dos años, pretende cuantificar la relación de la reproducción, muda y movimientos de poblaciones de colibríes con las épocas de floración de sus plantas alimenticias, en La Montura, un sitio de la selva lluviosa premontana a 1.000 m de altura en la ladera caribeña costarricense. La comunidad está compuesta por 22 especies de colibríes (9–10 residentes; 5–6 visitantes regulares estacionales y el resto raros o accidentales) que visitan en forma colectiva el menos 70 especies de plantas, de las cuales polinizan casi 50.

Los patrones de las aves para visitar las flores, permiten dividir la comunidad en subcomunidades, cada una con su propio ritmo estacional. Estas son: a—Subcomunidad Pico de Lanza: el pico de lanza mayor (*Doryfera ludovicae*) y cinco especies de arbustos epífitos grandes y probablemente varias bromelias. Esta subcomunidad está caracterizada morfológicamente por el pico largo fino y casi recto, que corresponde con la forma del tubo de las corolas de las flores. Las cinco plantas principales de alimentación florecen en secuencia casi perfecta a lo largo del período de estudio; la temporada de reproducción de *D. ludovicae* coincide con la gran abundancia de flores; la muda con disponibilidad intermedia de flores. b—Subcomunidad Ermitaño: Comandada por el ermitaño verde (*Phaethornis guy*) con su pico largo, curvado hacia abajo y 19 flores con sus corolas de forma similar del sotobosque ("understory") y del subdósel bajo las copas de los árboles ("subcanopy"). La disponibilidad de flores es alta durante la reproducción, teniendo su pico máximo durante el período en que la muda y reproducción se superponen, y declina durante la muda y los períodos de poca actividad ("quiescent"); las especies *Heliconia* parecen proveer recursos de néctar críticos para reproducir. Las plantas de las cuales se alimenta *P. guy* florecen en secuencia una tras otra cuando se analizan separadamente los períodos de reproducción y no-reproducción del ave. También se incluye acá al Pico de hoz colioliva (*Eutoxeres aquila*) cuyas visitas al área de estudio entuvieron relacionadas al florecimiento de una sola planta de alimentación. c—Subcomunidad *Heliodoxa-Marcgravia*: el colibrí jacula (*Heliodoxa jacula*) y tres especies de *Marcgravia*, polinizadas por polillas de la familia Sphingidae o murciélagos, sobre las cuales parece estar basado el ciclo de reproducción y muda del ave. Las tres especies de *Marcgravia* florecen en una secuencia que es utilizada por *H. jacula*, pero esto no refleja una relación de coevolución, ya que el colibrí es un ladrón de néctar. d—Subcomunidad "Generalizada": varios picaflores de tamaño pequeño a mediano, de pico recto y flores de corola recta corta o mediana. En este grupo existe suficiente superposición en las visitas a las flores, lo cual imposibilita mayores subdivisiones. Las principales especies de picaflores (*Lampornis hemileucus*, *Eupherusa nigriventris*, *Elvira cupreiceps*) reproducen en asociación íntima con una serie de epífitas de las copas de los árboles mayormente de la familia Ericaceae. Muchos individuos de estas dos últimas especies, además de *Colibri delphinae* emigran luego de la reproducción o como máximo cuando comienza la muda; sus lugares son ocupados por varias especies de vistantes post-reproductivos de otras elevaciones, que mayormente utilizan las flores abundantes del arbólito *Cephaelis elata*, del nivel de vegetación inferior.

La mayoría de los picaflores de La Montura reproducen desde la mitad o final de la estación húmeda hasta el principio de la temporada seca, aproximadamente desde octubre hasta marzo y mudan desde marzo hasta junio, cuando comienza la estación de las lluvias. Machos de muchas especies mudan uno o dos meses antes que las hembras. El ciclo de *H. jacula* está desplazado de uno a dos meses antes que el de la mayoría de las especies, mientras que el de *P. guy* es casi lo opuesto: reproduce entre abril y septiembre y muda entre julio y noviembre. Las diferencias en las estaciones en otras comunidades de flores y picaflores refleja régimenes climáticos diferentes y afinidades taxonómicas por ejemplo en todas las áreas las Ericáceas florece mayormente en la estación húmeda y *Heliconia* de junio a agosto.

Las diversas comunidades de flores y picaflores en los bosques húmedos de Costa Rica muestran divisiones en subcomunidades similares, habiendo diferentes riquezas de especies y afinidades taxonómicas. En bosque seco y vegetación secundaria, la mayoría o todas las especies pertenecen a la subcomunidad generalizada. La relación entre la interacción planta-polinizador y temporada de floración está reevaluada a la luz de los cambios en las demandas de néctar de las aves debido a la reproducción y muda. Se concluye que la competencia por polinizadores puede ser una fuerza selectiva de importancia en la temporada de estaciones de floración, pero cuya intensidad varía de acuerdo con el ciclo anual de los polinizadores, y no puede ser

propriamente determinado sin tomar en cuenta la biología de los polinizadores. Finalmente basándose en evidencias ecológicas y biogeográficas, se discute que muchas (pero por cierto no todas) las interacciones ave-flor en la comunidad de La Montura representan verdaderos mutualismos coevolucionados.

Communities of tropical birds have well-defined seasonal rhythms of reproduction, molt, and population movements just as do avifaunas of higher latitudes (Skutch 1950; Fogden 1972). In tropical communities, however, there is no overriding zeitgeber corresponding to the annual photoperiodic (and related temperature) cycle. Seasonal changes in the avifauna, as well as in the resources required by the various bird species, are thus related in large part to patterns of rainfall. Different resources (insects, flowers, fruit, etc.) often peak at different times, or show different patterns of availability in different years, reflecting variability in rainfall (Stiles 1978; Wolda 1978).

Interpretation of avian seasonal rhythms may be facilitated if the birds' critical resources can be specified and counted with relative precision. This is possible with hummingbirds, whose critical energetic resource, nectar, comes in conspicuous, stationary, countable packages with a predictable daily pattern of energy yield (cf. Wolf et al. 1972, 1975; Stiles 1975; Feinsinger 1976). Although small insects and spiders are nutritionally important to hummingbirds (e.g., Scheithauer 1966), there is no evidence that these resources are limiting for the performance of seasonal activities like breeding and molt, which have been shown to be strongly influenced by flowering patterns (Skutch 1950; Stiles 1978, 1980). Therefore, detailed data on flowering phenology and flower visitation by the birds are required to compare seasonal patterns in different hummingbird communities.

When such data exist for several hummingbird-flower communities in a single region, several interesting questions can be addressed. Are flowering patterns similar or offset in different communities? How does this affect breeding, molting, and seasonal movements of the hummingbirds? Does a given plant species or group respond similarly in different communities to a given set of environmental conditions (especially rainfall)? How much variation exists between communities in flower choice by hummingbirds or in plant-pollinator specificity? Are certain taxonomic or ecological groups of flowers of outstanding importance to the hummingbirds, and how do these vary with parameters such as elevation and moisture?

Previously I studied a tropical wet lowland hummingbird-flower community (Stiles 1978, 1980; Stiles and Wolf 1979), and participated in a study of a high-montane community (Wolf et al. 1976). Comparisons of the two communities were hindered, however, by the complete lack of taxonomic overlap between them. Accordingly, I initiated a study of hummingbird-flower communities at middle elevations. In this paper, I present data gathered at the first such site, La Montura (elev. = ca. 1000 m) on the Caribbean slope of the Cordillera Central of Costa Rica. I make preliminary comparisons between the seasonality of this hummingbird-flower community, and those of Finca La Selva (elev. = ca. 100 m, at the foot of this cordillera), and Cerro de la Muerte (elev. = ca. 3000 m at the crest of the Cordillera de Talamanca, the next mountain range to the south), as well as to the second-growth, middle-elevation community at Monteverde (elev. = ca. 1100 m in the Cordillera de Tilarán in northwestern Costa Rica), studied by Feinsinger (1976, 1977, 1978).

METHODS

STUDY AREA

The present study was carried out at La Montura ($10^{\circ}7'N$, $83^{\circ}58'W$) in Parque Nacional Braulio Carrillo, a 32,000 ha reserve centered around Volcán Barba in the Cordillera Central of Costa Rica. The topography of the La Montura area is rugged, characterized by long steep-sided ridges that extend down from the continental divide. The tops of the ridges are relatively gently sloping, but their sides drop off precipitously into deep canyons containing narrow, rocky rivers that flow swiftly northward toward the Caribbean coastal plain (Fig. 1). The ridge of La Montura divides the watersheds of the Río Patria to the west and the Río La Honduras to the east.

Most of my observations were made along ca. 2.5 km of study trails, chiefly within a roughly rectangular area some 12 ha in extent, just east of the ridgeline. The study area has a mean elevation of ca. 1000 m, with extremes of 900 and 1070 m; its topography is varied, including



FIG. 1. Above: General aspect of topography and vegetation at La Montura. View from upper part of the study area, looking east across the Río Patria drainage. Below: View of forest understory at La Montura. Note the dominance of dicot shrubs, large-leaved monocots (palms, *Heliconia*, etc.), and tree-ferns.

steep slopes and ravines, level areas, and both permanent and intermittent streams. Except for a small area along a now-abandoned road at one corner, the entire area is covered with primary forest. Perhaps the most striking feature of the La Montura forest is the abundance and diversity of epiphytes. Many trees support huge masses of moss, aroids, cyclanths, large

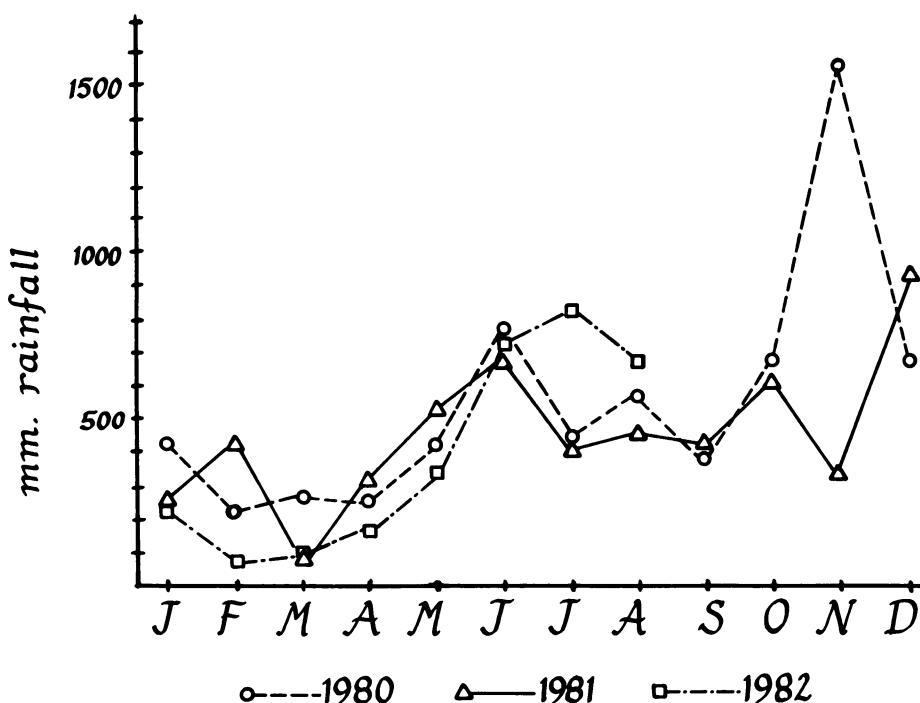


FIG. 2. Rainfall recorded at Cariblanco, ca. 30 km E of La Montura, 1980–1982.

hemiepiphytes like *Clusia*, epiphytic shrubs (e.g., Ericaceae, Gesneriaceae), and vines (e.g., Marcgraviaceae). Bromeliads and orchids are also common but do not dominate the epiphyte flora to the extent that they do in some lowland forests (e.g., Gentry 1982). The forest canopy is quite irregular; large trees reach 35–40 m, but treefalls are frequent as a result of heavy rains followed by high winds. Light gaps of various sizes and ages are thus common in the understory, which is dominated by tall shrubs (notably Rubiaceae, Gesneriaceae), palms, treeferns, and large herbs such as *Heliconia* and *Calathea* (Fig. 1).

The area of La Montura is mapped as Premontane Rain Forest in the Holdridge Life Zone System (Tosi 1969), but unfortunately precise weather data for the area do not exist. The closest weather station is at Guápiles, ca. 20 km northeast but at a much lower elevation (300 m) at the edge of the coastal plain. The station with the most comparable weather is at Cariblanco, some 30 km to the northeast but similar in elevation and topographic situation. The Cariblanco rainfall data correspond well with my subjective impressions of La Montura rainfall, and I consider them representative of the latter for purposes of comparison. The driest months at Cariblanco are February and March, although only in 1982 was the dry season well marked. Over the rest of the year rainfall is heavy, especially from June to August and October to December. In both years of my study more than 6 m of rain probably fell at La Montura (Fig. 2). Average daytime temperatures reached ca. 24°C and nighttime temperatures averaged about 15°C at Cariblanco.

FIELD WORK

Between late June 1980 and late May 1982, I made 21 two- to seven-day visits to La Montura, at intervals of four (when possible) to six weeks. During each visit, I estimated the numbers of all species of flowers visited by hummingbirds within 10 m of all study trails (exact counts were impossible for many canopy species). I also noted whether flowering was increasing or decreasing, based upon the relative numbers of unopened buds, open flowers, and developing fruits. I had great difficulty in identifying and counting hummingbirds in the dense, epiphyte-laden canopy, especially under the foggy to drizzly conditions that often prevailed. I therefore concluded that an overall subjective estimation of hummingbird abundance, based upon mist-net data and all visual observations, would be little less accurate (and

potentially far less misleading) than numbers derived from ground-based censuses. Abundance of each species was evaluated according to a semiquantitative scale running from 0 (= absent) and 1 (= rare) to 5 (= very abundant). I also recorded all hummingbird visits to flowers, where both bird and plant could be identified.

Mist-nets set 0 to 3 m above ground were used to sample hummingbird populations. I tried to accumulate ca. 300 net-hours per visit, but this was often impossible due to rainy weather. Each hummingbird was marked with a colored plastic tag (Stiles and Wolf 1973) or an aluminum leg band with photoengraved letters. Birds were weighed to the nearest 0.1 gm with a Pesola spring balance, and measured (exposed culmen, wing chord, tail length) to within 0.5 mm with a millimeter rule. Each individual was also checked for molt, which was scored according to the system of Stiles and Wolf (1974). Young birds were diagnosed by distinctive plumages (cf. Ridgway 1911) or by striations in the maxillary ramphotheca (Ortiz-Crespo 1972). Breeding females could be recognized as such by the presence of a brood patch, although this is less obvious in hummingbirds than in most birds, because few or no feathers are lost when it is formed. However, the skin does become noticeably thickened and crinkly, and more bluish or grayish in color. All available means were used to determine the breeding seasons of the La Montura hummingbirds: observations of females carrying nesting material or feeding fledglings, the nests themselves, the presence of brood patches on females, and bill striations on juveniles.

I attempted to collect vouchers for identification of all plant species whose flowers were visited by hummingbirds, but this was impossible for some epiphytes and trees. To characterize flower size, I defined "effective corolla length" as the minimum distance between the mouth of the corolla tube and the nectar chamber. I was unable to obtain quantitative samples of daily nectar production for most species, particularly epiphytes. However, by considering such parameters as flower size, dimensions of the nectar chamber, and data from related species, I usually was able to categorize the daily nectar flow as "low" ($<20 \mu\text{l}/\text{flower/day}$) or "high" ($\geq 20 \mu\text{l}/\text{flower/day}$). For evaluating blooming seasonality, I used either the actual flower counts or a simplified measure derived therefrom, the number of species in "good bloom," defined as those species attaining 50% or better of the maximum flower count in a given blooming season.

Vouchers of plants collected are deposited in the herbaria of the Universidad de Costa Rica and/or the Museo Nacional de Costa Rica. I also collected vouchers of most species and plumage types of hummingbirds, but I did not attempt to obtain series of specimens for gonad analysis. Bird specimens are deposited in the Museo de Zoología, Universidad de Costa Rica.

DATA ANALYSIS

To evaluate the relation between flowering parameters and hummingbird activities, I calculated non-parametric correlation coefficients (Spearman's r_s) between the number of flowers or the number of species in good bloom, and the total hummingbird abundance (according to the semi-quantitative system above) or the number of species breeding, for each census period. For single hummingbird species, I compared the numbers of flowers available on censuses during the bird's breeding, molting, and quiescent (neither breeding nor molting) periods with Kruskal-Wallis nonparametrical analysis of variance (Zar 1974).

I also tested statistically whether the periods of good bloom of the flowers used by particular hummingbird species were random, aggregated, or hyperdispersed. By interpolation from the flower counts (including my estimation of the direction of flowering—increasing or decreasing), I determined whether a given flower species was in good bloom during each 2-week interval of the study period. I then summed the number of intervals with 0, 1, . . . , N species in good bloom (N = the total number of species used by the hummingbird in question) and determined the mean \bar{n} number of species in good bloom per interval. If blooming periods are randomly distributed, the number of intervals with 0, 1, . . . , \bar{n} species in good bloom should approximate a Poisson distribution with mean \bar{n} . Chi-square tests were used to test for goodness of fit between the expected (Poisson) and observed distributions. The direction of any deviation from randomness is given by the variance : mean ratio (Zar 1974).

While a detailed analysis of flower choice by the hummingbirds is beyond the scope of this paper, some means of comparing the visitation patterns of different species was required for the purpose of defining subcommunities. To this end I calculated overlap values using the formula of Feinsinger (1976) between each pair of resident hummingbird species over all flower species throughout the study period. If the mean overlap of any species or group of

TABLE 1
STATUS, ABUNDANCE, AND PHYSICAL CHARACTERISTICS OF LA MONTURA HUMMINGBIRDS¹

	Status ²	Max. abund. ³	No. banded	\bar{X} wt. ⁴	\bar{X} bill length ⁴	Bill ⁵ curv.
Hermits (Phaethorninae)						
<i>Eutoxeres aquila</i> (Ea): White-tipped Sicklebill	R?	U	25	10.7	32.2	V
<i>Phaethornis guy</i> (Pg): Green Hermit	R	A	113	6.0	40.9	M
<i>P. longuemareus</i> (Pl): Little Hermit	V	R	3	2.6	21.2	S
<i>Threnetes ruckeri</i> (Tr): Band-tailed Barbthroat	V	X	1	5.6	30.1	S
Nonhermits (Trochilinae)						
<i>Amazilia saucerrottei</i> (As): Steely-vented Hummingbird	V	X	1	4.8	18.7	O
<i>Campylopterus hemileucurus</i> (Ch): Violet Sabrewing	N	U	5	10.7	31.4	S-M
<i>Colibri delphinae</i> (Cd): Brown Violet-ear	B	C	6	6.5	16.8	O
<i>C. thalassinus</i> (Ct): Green Violet-ear	N	U	8	5.4	21.3	O-S
<i>Discosura conversii</i> (Pc): Green Thorntail	R?	R?	2	3.0	12.0 ⁶	O
<i>Doryfera ludovicae</i> (Dl): Green-fronted Lancebill	R	U	17	5.7	34.4	S'
<i>Elvira cupreiceps</i> (Ec): Coppery-headed Emerald	R	C	52	3.3	14.1	S
<i>Eupherusa nigriventris</i> (En): Black-bellied Hummingbird	R	A	71	3.5	14.9	O
<i>Florisuga mellivora</i> (Fm): White-necked Jacobin	V	X	1	7.0	18.1	O
<i>Heliodoxa jacula</i> (Hj): Green-crowned Brilliant	R	A	63	8.6	21.9	O
<i>Heliothryx barroti</i> (Hb): Purple-crowned Fairy	R	U	6	5.6	17.2	O
<i>Hylocharis eliciae</i> (He): Blue-throated Goldentail	V	X	1	3.7	17.6	O
<i>Klais guimeti</i> (Kg): Violet-headed Hummingbird	V	R	2	2.8	13.2	O
<i>Lampornis calolaema</i> (Lc): Purple-throated Mountain-gem	N	U	6	5.4	19.4	O
<i>L. hemileucus</i> (Lh): White-bellied Mountain-gem	R	A	75	5.5	19.3	O
<i>Lophornis heleneae</i> (Loh): Black-crested Coquette	V?	X	0	2.9	11.3 ⁶	O
<i>Microchera albocoronata</i> (Ma): Snowcap	V	R	2	2.5	11.9	O
<i>Thalurania colombica</i> (Tf): Crowned Wood-nymph	N	C	12	4.3	20.1	O

¹ Abbreviations for species (in parentheses) are used in figures.

² R = resident (most or all year); B = breeding resident; N = regular nonbreeding resident; V = vagrant or stray.

³ A = abundant; C = common; U = uncommon; R = rare; X = fewer than three records.

⁴ Mean of all birds banded; weights in grams; bill length in mm. Birds from other sites included if the sample size was very small.

⁵ V = very strongly curved; M = moderately curved; S = slightly curved; O = straight; S' = slightly recurved.

⁶ Data from Ridgway (1911).

species with all other species is less than 0.1, I consider that species (or group) to constitute a subcommunity. The value of 0.1, while arbitrary, is reasonably in accord for values between "coexisting specialists . . . whose specialties do not overlap extensively" (Feinsinger 1976: 282).

COMMUNITY COMPOSITION

HUMMINGBIRDS

To date, 22 species of hummingbirds have been recorded at La Montura (Table 1). Eight are rare to accidental visitors whose effects upon the dynamics of the community are negligible. Most of these are vagrants from lower elevations on the Caribbean slope, but one species, *Amazilia saucerrottei*, evidently strayed across the continental divide from the deforested Valle Central. Four species are regular visitors in good numbers; one of these (*Thalurania colombica*) moves uphill, while the remaining three move down from higher elevations. Taken as a whole, these visitors appear mainly in the early- to mid-rainy season, with peaking in June and July (Fig. 3). The presence of most of these species is associated with the flowering of *Cephaelis elata* (Rubiaceae), an abundant understory treelet. Individuals of these species netted in the study area were mostly immatures, with a few molting adults. This suggests that these species invade La Montura following their respective breeding seasons in other areas.

The remaining 10 species are present at La Montura for much or all of the year and are known or suspected to breed there (or nearby); they comprise the area's "nuclear" hummingbird community. Of these species, the status of *Discosura conversii* is least certain. This small species seems restricted to the upper canopy and may be more numerous than infrequent sightings suggest. It is very rarely captured in mist-nets, and I lack firm data on breeding and

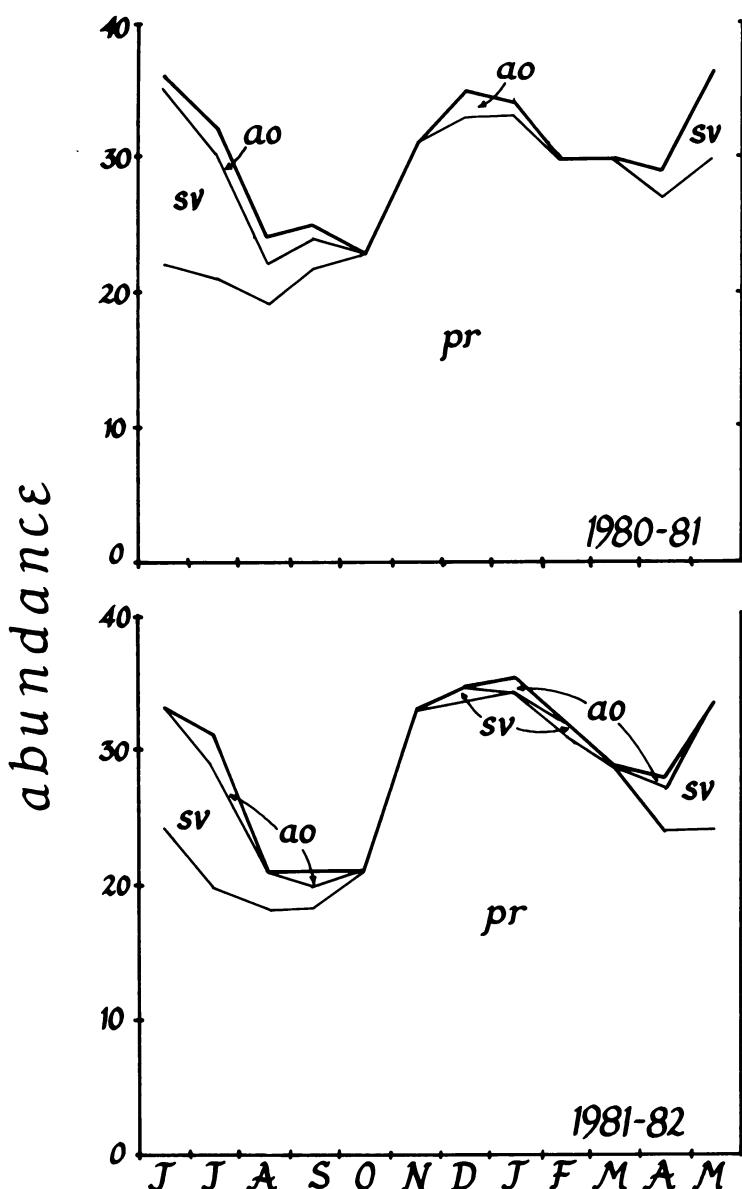


FIG. 3. Hummingbird abundance at La Montura during the two years of this study, according to the semiquantitative system presented in the text. pr = permanent residents and breeding residents; sv = nonbreeding seasonal visitors; ao = accidentals and occasional visitors.

molt. Nevertheless, it seems to be present in most months, and I have seen possible breeding displays by males in December and March. The other marginal species is *Eutoxeres aquila*, which reaches its upper elevational limit at La Montura. I found no evidence of its nesting on the study area, although a few individuals could be seen or netted at any time of year. Given the extremely powerful flight of this large species, it is possible that the birds of the study area, including females with brood patches, might be commuting from lower elevations on a daily basis.

The numerically dominant species of the community are *Phaethornis guy*, *Lampornis hemileucus*, and *Heliodoxa jacula* on a year-round basis, although each shows seasonal fluctuations

in abundance. Species that are abundant at certain seasons but rare or absent at others include *Elvira cupreiceps* and *Euperusa nigriventris*. Such a pattern is also shown by *Colibri delphinae*, which however, is never as numerous as the two preceding species. Present year-round in smaller numbers are *Heliothryx barroti* and *Doryfera ludovicae*. Morphologically, the nuclear community consists of two hermits, one very large and with a very strongly curved bill (*E. aquila*), and one medium-sized, with a less decurved but very long bill, and six nonhermits. One of the latter has a very long, slender, slightly upturned bill (*D. ludovicae*); four are of medium to rather large size with straight bills of rather intermediate lengths; three are small-sized and short-billed (Table 1). The implications of these patterns will be considered below.

Relatively few species are strictly confined to a particular forest stratum at La Montura, and most species occur in edge habitats (e.g., light gaps, streams). For example, *P. guy* ascends freely into the lower canopy at times to visit flowers, unlike its congener *P. superciliosus* at lower elevations (Stiles 1980). Individuals of species such as *E. nigriventris* move freely between canopy and understory, feeding largely in the former and singing or nesting in the latter. Often males tend to occur more in the canopy, and females in the understory, but both sexes (notably of *E. cupreiceps*, *L. hemileucus*) may mix at patches of flowers in either. For hummingbirds such as *H. jacula* and, to some extent, *E. cupreiceps* and *L. hemileucus*, the preferred foodplants themselves occur at a wide range of heights above ground (see below). These patterns doubtless reflect the broken, irregular canopy of the La Montura forest. Only *D. ludovicae*, *C. delphinae*, and *D. conversii* seem confined to the canopy in this forest; only *E. aquila* is restricted to the understory (Table 1).

FLOWERS

The flowers of well over 60 species of plants are more or less regularly visited by hummingbirds at La Montura (Appendix I). At least 50 species are pollinated primarily by hummingbirds. Fully half of these ornithophilous species are epiphytes. Shrubs and large terrestrial herbs are represented by 10 or more species each, while the remaining species include a few vines and (mostly small) trees. The list of non-ornithophilous flowers at which hummingbirds forage also includes a high proportion of epiphytes, and relatively more trees. This list is decidedly incomplete, due in part to the difficulty of obtaining specimens of many trees and epiphytes for identification. Many such species are also visited only infrequently or irregularly, depending upon what else is in bloom.

The great majority of the hummingbird-pollinated flowers of La Montura are concentrated in a few plant families: Musaceae (= Heliconiaceae of some authors), Bromeliaceae, Gesneriaceae, and Ericaceae (Appendix I). If one considers numbers of flowers, the Musaceae and Bromeliaceae decline in overall importance, while the Ericaceae is easily the most important family, followed by the Rubiaceae, Gesneriaceae, and Acanthaceae. Other parameters useful to consider are corolla length (and to a lesser extent curvature) and nectar production. Some families can be characterized by a particular combination of these characters (e.g., all Musaceae have relatively high nectar production and long corollas), whereas others (e.g., Gesneriaceae, Ericaceae) are much more heterogeneous. Taking the plant species visited (Appendix I) as a whole, there is a highly significant positive association between corolla length and nectar production, and a highly significant negative association between flower abundance and nectar production (Table 2). That is, the most abundant flowers tend to be those with short corollas and low nectar production; flowers with long corollas and high nectar production tend to be scarce overall, although they may occur in relatively large clumps (e.g., *Satyria warsewiczii*). Most species of hummingbird foodplants at La Montura have a single discrete flowering peak each year. Certain families tend to have more irregular patterns of flowering (especially the Bromeliaceae), but there is no obvious association between the type of blooming seasonality and either corolla length or nectar production (Table 2, Appendix I).

SEASONAL PATTERNS IN THE COMMUNITY

HUMMINGBIRD NUMBERS, BREEDING, AND MOLT

Overall hummingbird numbers were consistently high through most of the year, roughly from November through July, and rather sharply lower between about August and October (Fig. 3). However, patterns of abundance varied considerably among different members of the community. Some species were relatively common year-round, albeit less numerous in some months than others. For instance, *P. guy* was less numerous between about December and April; *L. hemileucus* declined somewhat between August and October. Seasonal fluctua-

TABLE 2
RELATION BETWEEN DAILY NECTAR SECRETION AND EFFECTIVE COROLLA LENGTH, PEAK
FLOWER ABUNDANCE AND BLOOMING SEASONALITY OF 40 SPECIES OF HUMMINGBIRD
FOODPLANTS AT LA MONTURA

Nectar secretion ¹	Flower characteristics				
	Effective corolla length (mm) ¹				
	<10	10–19	20–29	30–39	≥40
Low	4	14	2	1	0
High	0	0	4	11	4
χ^2 (combining species above and below 20 mm) = 26.78; $P < 0.0001$					
Maximum flower count in censuses ¹					
	<10	10–100	101–1000	>1000	
Low	1	8	7	5	
High	3	13	3	0	
χ^2 (combining species above and below 100 flowers) = 5.63; $P < 0.05$					
Type of blooming seasonality ¹					
	A ₁	A ₂	B ₁	B ₂	C
Low	14	0	1	1	2
High	9	3	3	0	3
					D
					3
					1

¹ As in Appendix I.

tions in the numbers of other species, notably *Elvira cupreiceps*, *Eupherusa nigriventris*, and to some extent *Heliodoxa jacula*, were more marked. All of these species are consistently abundant at certain times of year; the timing and extent of their periods of relative scarcity seem more variable. For instance, *P. guy* decreased on the study area in late November in 1980–1981, but not until about mid-January in 1981–1982. Similarly, in 1981 the declines in *E. nigriventris* and *E. cupreiceps* occurred about early- to mid-July; in 1982, they occurred in April. *Eutoxeres aquila*, *D. ludoviae*, and *H. barroti*, were never very numerous, but were evidently present year-round. The short-term visitors varied considerably in both numbers and timing of their visits on a year-to-year basis. Both *T. colombica* and *C. hemileucurus* were more numerous and stayed longer in the area in 1980 than in 1981; *L. calolaema* appeared in April 1982, but not until June in 1981. Taken as a whole, the peak abundance of these visitors was June–July. The overall abundance of hummingbirds in the community changed rather little, however, as several resident species declined at this time. The August to October low point of hummingbird abundance resulted from the gap between the departure of these visitors, and the return to the area of large numbers of resident species such as *E. nigriventris* and *E. cupreiceps* (Fig. 3).

The peak breeding season for most La Montura hummingbirds was about November to March, with breeding commencing sometime between August and October; virtually all these species ceased breeding by April (Fig. 4). The breeding season of *H. jacula* was slightly earlier, roughly late July through December or January. *Phaethornis guy*, however, departs completely from this pattern, with a breeding peak from about April through August. I lack adequate information on breeding by *E. aquila*, *H. barroti* and *D. conversii*. At La Montura, a female *H. barroti* with nesting material was seen in September 1980; female *Eutoxeres* with brood patches were netted mostly from January through March (but also one in May and one in July). At Finca La Selva in the lowlands, *E. aquila* definitely breeds between December and February, and *H. barroti* between July and October (Stiles 1980, unpubl. data).

As is usual in hummingbirds, molt followed immediately after breeding in most or all species at La Montura (Fig. 5). Most species began molt in February or March, *H. jacula* as early as late November. Perhaps because males have lower energetic demands than females during breeding, males of many species commenced molt one to two months ahead of females (January vs March in *L. hemileucus*, February vs March in *E. nigriventris*, March vs April in *E. cupreiceps*, November vs December or January in *H. jacula*). Only in *P. guy* was there some temporal overlap between molt and breeding, with a few individuals commencing molt

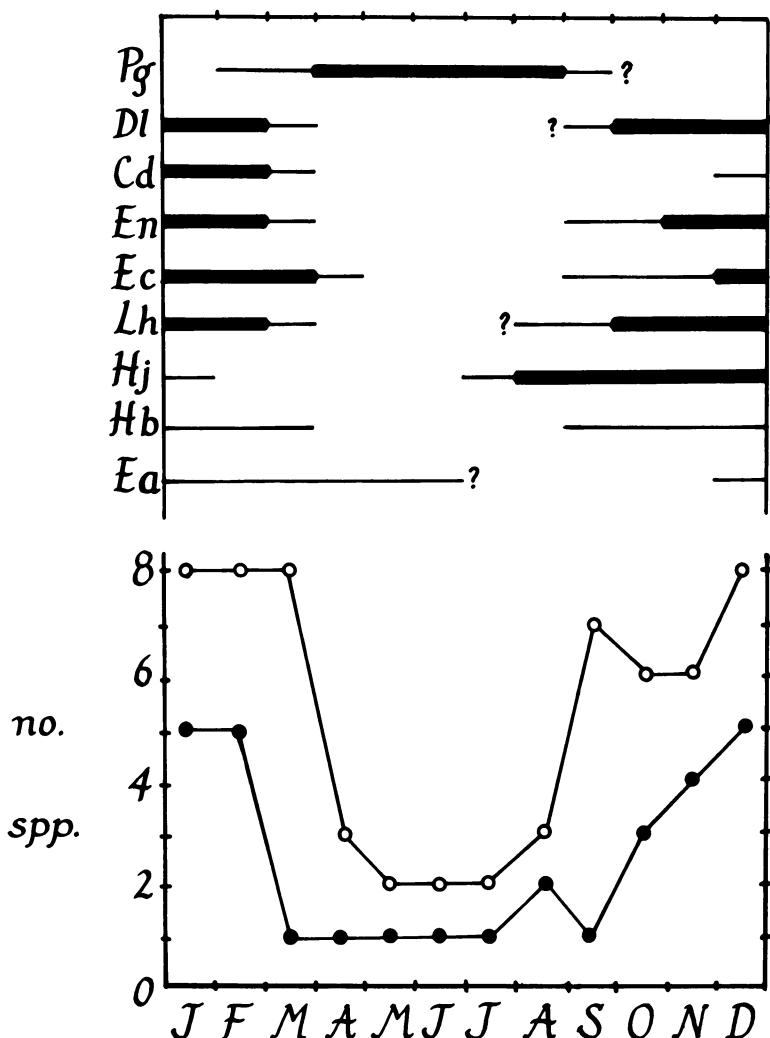


FIG. 4. Above: breeding seasons of La Montura hummingbirds; abbreviations for species as in Table 1. Heavy lines indicate peak of breeding season (insufficient data are available to determine breeding peaks in *E. aquila*, *H. barroti*). Below: number of species showing breeding activity (upper line) or at peak of breeding (lower line) in different months.

as early as late May or June. Overlap was at best slight for the bulk of the population, however, which showed a well-defined peak of molt from September to November–December.

I detected no significant between-year variation in the timing of molt for any species at La Montura. The timing of breeding did appear to vary somewhat from year to year, however. The breeding seasons of *L. hemileucus*, *E. cupreiceps*, *E. nigriventris*, and, perhaps, *H. jacula* all appeared to begin about a month earlier in 1980–1981 than in 1981–1982. In 1980, some *P. guy* continued breeding at least through October; in 1981, no breeding was detected after early- to mid-September. In general, more data are needed for a thorough evaluation of annual variation in breeding (or molting) seasonality in La Montura hummingbirds.

Population movements, particularly altitudinal migrations, seem to be characteristic of many hummingbirds at La Montura. The periods of lower abundance of many resident species result from partial or complete emigrations from the study area to lower elevations. For instance, *L. hemileucus* and *E. cupreiceps* regularly appear as low as 600 to 700 m during the

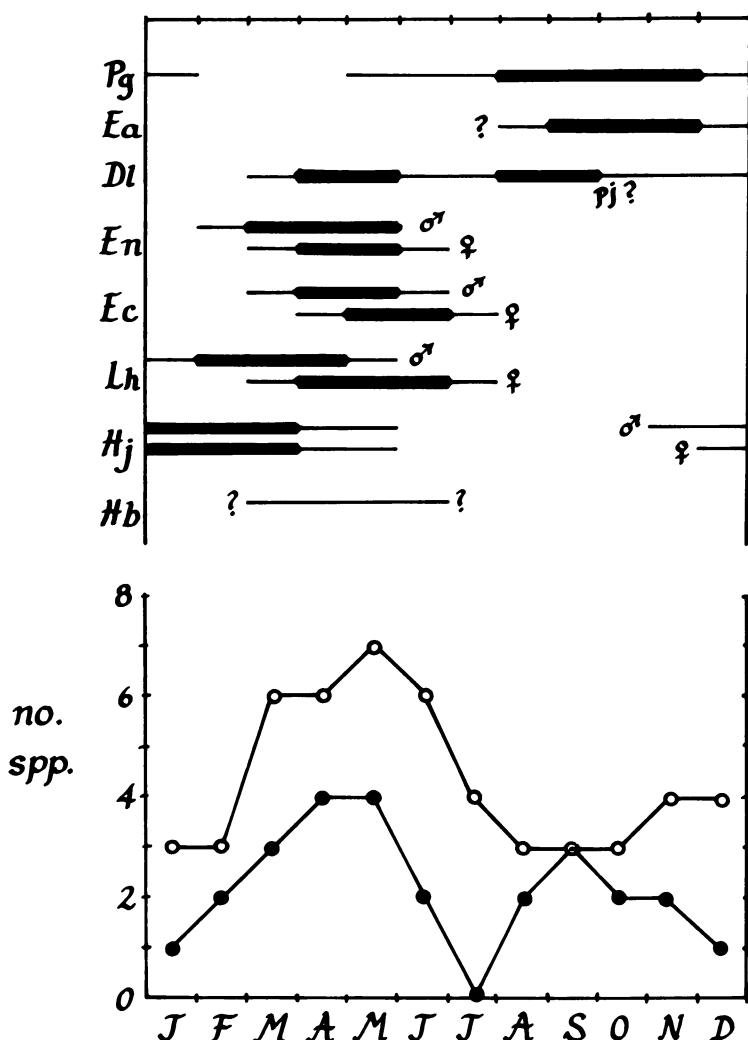


FIG. 5. Above: molting seasons of La Montura hummingbirds; abbreviations for species as in Table 1. Heavy line = peak of molting season (50% or more of all individuals mist-netted in molt); pj? = suspected postjuvenile molt. Lower: number of species showing some (upper line) or intense (lower line) molting activity in different months.

period when they are scarcest at La Montura. *Colibri delphinae* occurs at least occasionally as low as 75 m (Finca La Selva) in June and July, whereas *D. conversii* appears there in numbers from July through September of some years (Slud 1960, Stiles 1980). Small numbers of immature *P. guy* also appear at La Selva during these months; in view of the observed breeding season at La Montura, these birds probably represent post-fledging wanderers. Adult *P. guy* very rarely appear at such low elevations, and then only during the nonbreeding season (mostly December–February).

Influxes of several seasonal visitors definitely reflect altitudinal movements. The species that appear during the flowering of *Cephaelis elata* are drawn from several different elevational bands. *Thalurania colombica* breeds in the lowlands and foothills up to ca. 600 m, *C. thalassinus* in the mountains mostly above 2000 m (cf. Wolf et al. 1976), and *C. hemileucurus* at upper-middle elevations from ca. 1400 to 2300 m (pers. observ.). Elevational movements are strongly suspected, but not yet confirmed for some other species (e.g., *E. nigriventris*). Finally, movements of a few species seem to represent mainly nonaltitudinal shifts to other

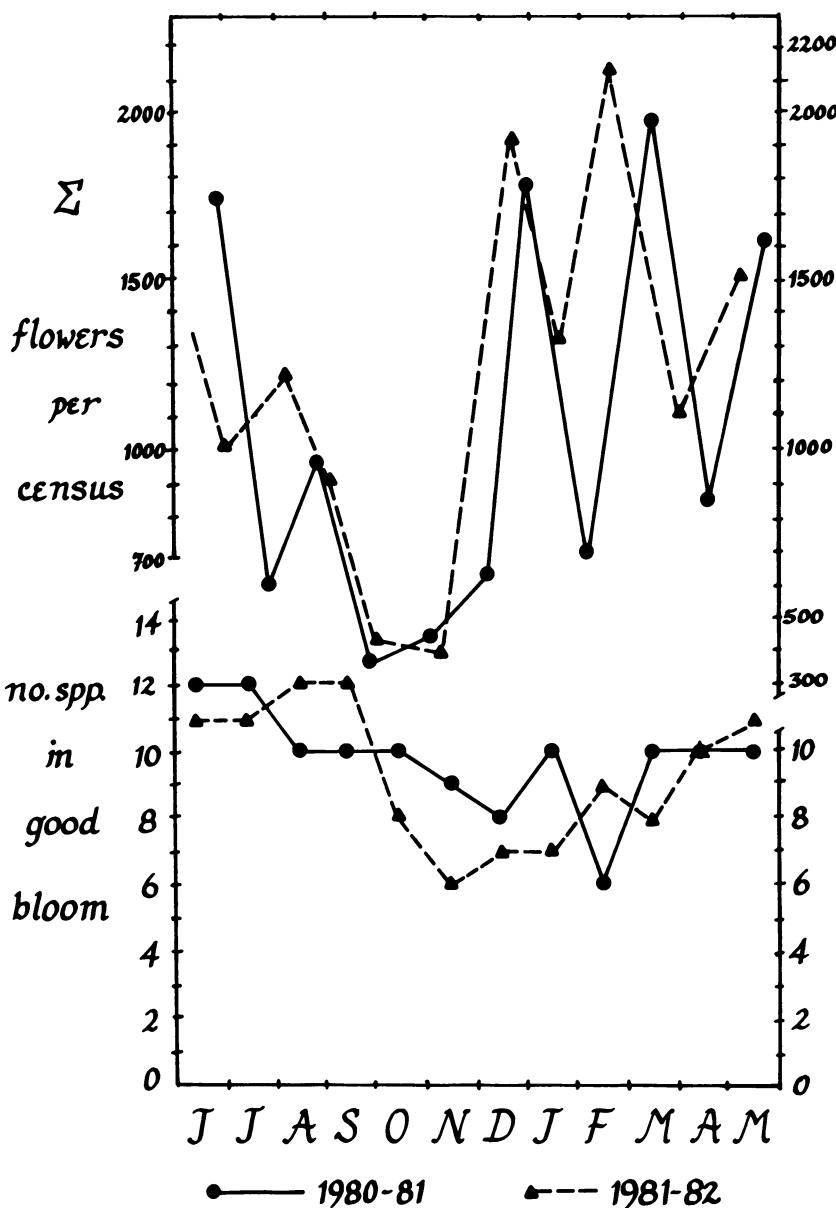


FIG. 6. Numbers of hummingbird-pollinated flowers recorded on flowering censuses at La Montura. Lower: number of ornithophilous plants in good bloom (see text) by month, June 1980–May 1982.

habitats where flowers not present on the study area occur. The scarcity of *H. jacula* in June and July reflects its departure to riparian habitats where *Heliconia latispatha* is in good bloom; it returns to the study area as blooming of this plant declines.

BLOOMING SEASONS OF HUMMINGBIRD FOODPLANTS

The numbers of ornithophilous plants in good bloom in the community were greatest in May and September, and lowest sometime between November and February (Fig. 6). However, the total number of hummingbird-pollinated flowers present at a given time showed a very different pattern, being lowest around October–November, and relatively high, but widely fluctuating, between about December and June (Fig. 6). The lack of correlation between these

TABLE 3
CORRELATIONS BETWEEN HUMMINGBIRD BREEDING AND ABUNDANCE, AND FLOWERING
PARAMETERS

	r_s^1
Entire Community	
Total no. of flowers vs total hummingbird abundance	.419*
No. spp. in good bloom vs total hummingbird abundance	-.250
Total no. of flowers vs no. breeding hummingbird spp.	.196
No. spp. in good bloom vs no. breeding hummingbird spp.	-.710**
No. spp. in good bloom vs total number of flowers	-.132
Lancebill Subcommunity ²	
Total no. of flowers (including bromeliads) vs abundance of <i>D. ludovicae</i>	.366
No. flowers of 5 principal foodplants, only, vs abundance of <i>D. ludovicae</i>	.440*
Hermit Subcommunity ²	
Total no. of flowers vs abundance of <i>P. guy</i>	.502*
No. of <i>Heliconia</i> flowers vs abundance of <i>P. guy</i>	.706**
No. flowers of <i>Centropogon</i> flowers vs abundance of <i>E. aquila</i>	.643**
No. <i>Centropogon</i> plus <i>Heliconia trichocarpa</i> flowers vs abundance of <i>E. aquila</i>	.652**
Generalized Subcommunity ²	
Total no. of flowers vs total hummingbird abundance	.784**
Total no. of flowers vs no. breeding hummingbird spp.	.482**
No. flowers of epiphytes only vs abundance of breeding hummingbird spp.	.799**
No. flowers of epiphytes only vs no. breeding hummingbird spp.	.819**
No. flowers of <i>Cephaelis</i> vs abundance of seasonal visitors	.572**
No. spp. breeding vs abundance of breeding hummingbird spp.	.785**
Abundance of seasonal visitors vs abundance of breeding spp.	-.350

¹ r_s = Spearman nonparametric correlation coefficient. Total 21 censuses, thus 19 degrees of freedom for all tests. n.s. = $P > 0.05$;

* = $P \leq 0.05$; ** = $P \leq 0.01$.

² Total for these tests refers to total numbers within the particular subcommunity.

parameters (Table 3) suggests their inadequacy as indicators of relative resource availability to hummingbirds. Moreover, only a weak correlation exists between total flower availability and hummingbird breeding activity, and a strong negative correlation between the latter and the number of species in good bloom (Table 3). This result, at first unexpected, indicates that the community as a whole might not be the appropriate unit for analysis, as different segments of it might have rather different seasonal rhythms. The situation is further complicated by the fact that overall flowering patterns differed between the two years of the study.

HUMMINGBIRD-FLOWER SUBCOMMUNITIES

Certain flowers seem to be characteristically associated with certain hummingbird species that are usually (but not invariably) their primary pollinators. Other flowers are visited and pollinated by a much wider variety of hummingbirds (Appendix I). Conversely, the different hummingbird species overlap to varying extents in their patterns of flower visitation. These overlap values permit subdivision of the community into sets of birds that exploit similar sets of flowers; seasonal patterns in the birds can then be related specifically to the set of flowers used. By these criteria, the nuclear hummingbird community of La Montura includes a group of five species among which overlaps are moderate to high, and four species that overlap relatively little with this group or with each other (Fig. 7).

The five broadly overlapping species (*L. hemileucus*, *E. nigriventris*, *E. cupreiceps*, *C. delphinae*, and *D. conversii*) are all small to medium-sized (3–6 g) with short to medium-length (11–20 mm), straight bills (Table 1). All visit a rather wide array of flowers that have short to moderate-length corolla tubes, many of which are entomophilous (Appendix I). I have recorded each species visiting 10 or more flower species (except for *D. conversii*, for which I have few data).

Closest to the preceding "generalized" group is *H. jacula*, which visits many of the same flowers during part of the year. Between about August and February or March, however, nearly all of my foraging records for this species are at three species of *Marcgravia* that are

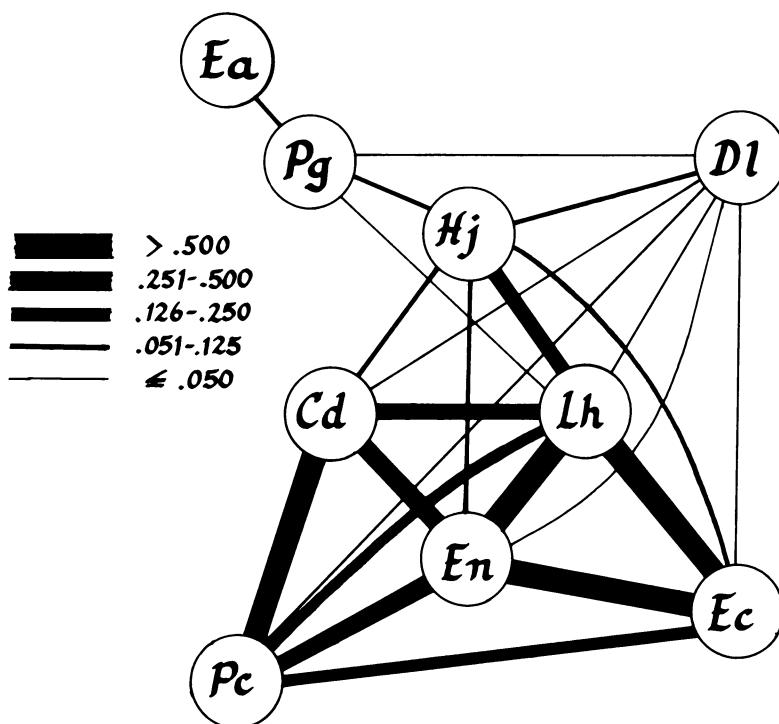


FIG. 7. Pairwise overlap values in flower visitation between all resident species of La Montura hummingbirds throughout the study period. For abbreviations of species see Table 1. Total number of flower visits for all species—786.

very rarely used by other hummingbirds. Thus, during these months one may define a *Heliodoxa-Marcgravia* subcommunity.

The two species of hermits clearly form a separate group. Overlap between them is low, because *E. aquila* visited only a very limited subset of the flowers visited by *P. guy*. However, since it visited no flowers not also visited by the latter, the two species are best included in the same subcommunity. *Doryfera ludovicae* is practically the sole visitor and pollinator of five species of canopy epiphytes with long corolla tubes. This hummingbird and its foodplants clearly constitute another recognizable subcommunity.

One species, the awl-billed *Heliothryx barroti*, was not included in the overlap analysis. This bird is a highly specialized, flower-piercing nectar thief. I know of no flower that it consistently pollinates. I have seen *H. barroti* rob flowers pollinated by hermits, lancebills, and members of the “generalized” group; thus, it could be considered to overlap all of these subcommunities. However, the subcommunities themselves presumably result from birds of similar morphologies (especially bill length and curvature) visiting flowers of corresponding corolla types (Snow and Snow 1972, 1980; Wolf et al. 1972). Since its feeding mode renders *H. barroti* essentially independent of floral morphology, I consider this species to exist outside of the system of subcommunities as such.

Lancebill subcommunity.—This clearly-defined grouping comprises the lancebill, *D. ludovicae*, and five species of epiphytic shrubs: the ericads *Satyria warsewiczii*, *Psammisia ramiflora*, *Cavendishia* sp., and *C. callista*, and the mistletoe *Psittacanthus nodosus*. Possible additional members of the subcommunity are five species of the bromeliad genus *Guzmania*. However, all of these latter are relatively scarce and bloom very irregularly, thus their importance to *D. ludovicae* is probably slight.

The most striking feature of the flowering of this subcommunity over the study period was its uniformity: major blooming peaks of the five principal foodplants were nearly perfectly staggered. In only five of the 48 sampling periods was no species in good bloom, and in only

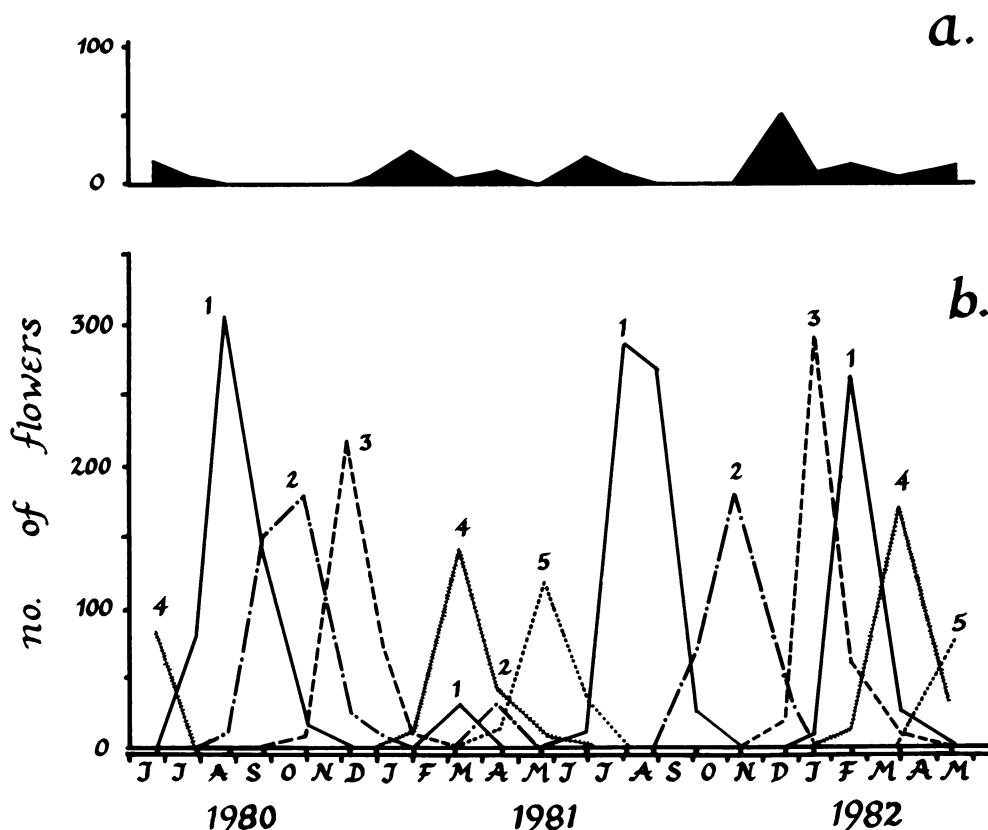


FIG. 8. Numbers of flowers recorded on different lancebill (*D. ludovicae*) foodplants during the study period. a. total for five species of *Guzmania* bromeliads; b. five principal species: 1 = *Satyria warsewiczi*; 2 = *Psittacanthus nodosus*; 3 = *Cavendishia* sp.; 4 = *Psammisia ramiflora*; 5 = *Cavendishia callista*.

seven were there as many as two (Fig. 8). This represents a highly significant deviation from a random distribution of flowering times, in the direction of overdispersion (Table 4). Because blooming peaks of different species involved different numbers of flowers, total flower availability to *D. ludovicae* fluctuated through the year. The breeding season generally coincided with periods during which flower availability was moderately (but not significantly) higher than it was during the nonbreeding season. A significant difference in flower availability did exist, however, between breeding, molting, and quiescent periods (Table 5). Flower availability was also significantly correlated with abundance of *D. ludovicae* on the study area (Table 3). Thus, it appears that the five epiphytic shrubs provide a dependable, staple year-round food supply to the lancebill, the major events of whose annual cycle are timed to fluctuations in this food supply.

Hermit subcommunity.—Of the two hummingbird species of this subcommunity, the Green Hermit is much more abundant, exploits many more species of flowers, and definitely breeds on the study area. Some 18–20 species of understory herbs and shrubs (including six species of *Heliconia*) are visited and pollinated principally or exclusively by *P. guy*. Although these foodplants collectively tend toward a uniform distribution of blooming seasons through the year, the difference from a random distribution is not significant (Table 4). Flower availability varies seasonally, with pronounced peaks in March to April and August to September (Fig. 9). These peaks are considerably less pronounced for nectar availability, however; the two species responsible for the high numbers of flowers, *Razisea spicata* and *Columnea macrophylla*, have less nectar per flower than other species of the subcommunity (Appendix I). Moreover, the flowers of *Razisea* in particular are often pierced and robbed by Bananaquits (*Coereba flaveola*) and other hummingbirds, notably *H. barroti*.

TABLE 4
**MEAN AND VARIANCE OF NUMBERS OF FLOWER SPECIES PER TWO-WEEK SAMPLING INTERVAL IN
 GOOD OR PEAK BLOOM IN DIFFERENT SUBCOMMUNITIES**

Subcommunity flowers and breeding period	No. sampling intervals	Measure of flowering	Mean no. spp. flowering	Variance : mean ratio	χ^2 ¹
Lancebill: 5 major flower spp., 1980–82	48	Peak bloom	0.83	0.27	31.90**
	48	Good bloom	1.04	0.26	30.81**
<i>Heliodoxa-Marcgravia</i> (3 spp.)					
1980–81	15	Good bloom	1.07	0.21	10.73**
1981–82	14	Good bloom	1.33	0.29	7.57*
Hermit: 18 spp. <i>P. guy</i> foodplants					
Entire 2 years	48	Peak bloom	2.31	0.81	2.37 n.s.
Entire 2 years	48	Good bloom	4.65	0.46	11.94 n.s.
Breeding-early molting periods only	35	Good bloom	5.14	0.28	20.25**
Late molt-nonbreeding periods only	13	Good bloom	3.00	0.18	9.19*
Generalized: 5 spp. canopy epiphytes during breeding season					
1980–81	13	Peak bloom	1.00	0.50	2.88 n.s.
	13	Good bloom	2.23	0.34	8.34*
1981–82	12	Peak bloom	1.42	0.83	0.71 n.s.
	12	Good bloom	2.42	0.34	4.97 n.s.

¹ χ^2 (Chi-square) test: Comparison of observed values with those expected according to Poisson distribution (see text). n.s. = $P > 0.05$; * = $P \leq 0.05$; ** = $P \leq 0.01$.

Both abundance and breeding of *P. guy* on the study area are positively associated with overall flower abundance, but even more closely associated with the numbers of *Heliconia* flowers (Tables 3, 4). Total flower availability is high during breeding but maximal in the period of molt-breeding overlap, much lower when the birds are only molting or quiescent (Table 4). Breeding of *P. guy* is specifically associated with high numbers of *Heliconia* flowers, suggesting that this hummingbird times its breeding cycle to the blooming of these flowers. Molt is mostly finished before the period of flower scarcity that begins in November or December (Figs. 6, 10).

The Sicklebill, *E. aquila*, is never numerous at La Montura, where it visits only the flowers of *Centropogon granulosus* and *Heliconia trichocarpa*. The former is visited relatively infrequently by *P. guy*, which is the chief visitor and pollinator of the latter. At both species *E. aquila* feeds by perching, grasping the inflorescence with its powerful feet; *P. guy* always hovers to feed. In no other hermit foodplants at La Montura is it possible for *E. aquila* to perch and reach the nectar with its strongly curved bill. The abundance of *E. aquila* at La Montura is positively correlated with flowering by *C. granulosus*; this correlation is scarcely improved if the flowering of *H. trichocarpa* is also considered (Table 3). However, the flowering of these plants and the putative breeding season of *E. aquila* do not correspond (Table 5). This strongly suggests that *E. aquila* does not breed at La Montura, and that the critical floral resources for breeding are found elsewhere, most likely at elevations below ca. 800 m, where *Heliconia longa* and *H. pogonantha*, both important foodplants for *E. aquila*, grow (Stiles 1975, 1979a).

Heliodoxa-Marcgravia subcommunity.—During much of the year, most of the activity of *H. jacula* is centered around the inflorescences of three species of *Marcgravia*. Each candelabra-shaped inflorescence of long-stalked flowers is subtended by a tube- or funnel-shaped bract into which the nectar is secreted. *Heliodoxa*, which like *E. aquila* has very powerful feet, perches on the bract or the flower stalks to feed. It is highly unlikely that *H. jacula* pollinates these species: anthesis occurs at or shortly before dusk; and the anthers have mostly fallen by dawn. I have seen the flowers of *M. schippii* being visited, and probably pollinated, by sphinx moths (*Eumorpha* sp.) after nightfall. However, these moths evidently do not use up the nectar in the bracts, which is harvested by *H. jacula* from dawn through mid-morning, and again in late afternoon prior to anthesis of the next crop of flowers. The significantly staggered sequence of flowering peaks shown by the three species (Fig. 10, Table 5), collectively spanned the period July through January in 1980–1981, and August through March 1981–1982; these months comprise the breeding season and at least the start of the molting season of *H. jacula*.

TABLE 5
COMPARISONS OF THE NUMBERS OF FLOWERS AVAILABLE TO DIFFERENT HUMMINGBIRD SPECIES WITHIN THEIR RESPECTIVE SUBCOMMUNITIES AT
DIFFERENT SEASONS¹

	Breeding			Molt			Quiescent			Statistic ²
	Breeding-molt overlap	Breeding	Molt	Breeding	Molt	Quiescent				
<i>P. guy</i> —all flowers	218.9 ± 94.2	380.8 ± 340.6	102.0 ± 51.6	115.6 ± 109.0	4.2 ± 2.0	H = 45.52**				
<i>P. guy</i> — <i>Heliconia</i> flowers only	51.1 ± 13.3	47.6 ± 19.8	8.4 ± 8.2	36.7 ± 23.8	36.7 ± 23.8	H = 78.71**				
<i>D. ludoviae</i> —5 principal spp.	190.0 ± 19.5	—	134.4 ± 78.1	—	—	H = 6.55*				
Nonbreeding										
<i>D. ludoviae</i> —5 principal spp.	190.0 ± 119.5	190.0 ± 119.5	365.5 ± 213.6	51.5 ± 15.3	37.8 ± 22.7	37.8 ± 22.7	115.6 ± 71.5	117.1 ± 86.9	117.4 ± 80.4	<i>U</i> _s = 24 n.s.
<i>D. ludoviae</i> —all spp.	190.0 ± 119.5	190.0 ± 119.5	365.5 ± 213.6	51.5 ± 15.3	37.8 ± 22.7	37.8 ± 22.7	115.6 ± 71.5	117.1 ± 86.9	117.4 ± 80.4	<i>U</i> _s = 28 n.s.
<i>P. guy</i> —all flowers	—	—	—	—	—	—	—	—	—	<i>U</i> _s = 16*
<i>P. guy</i> — <i>Heliconia</i> flowers only	—	—	—	—	—	—	—	—	—	<i>U</i> _s = 11*
<i>E. aquila</i> — <i>Centropogon</i> flowers	—	—	—	—	—	—	—	—	—	<i>U</i> _s = 42.5 n.s.
<i>E. aquila</i> — <i>Centropogon</i> plus <i>H. trichocarpa</i> flowers	—	—	—	—	—	—	—	—	—	<i>U</i> _s = 60 n.s.

¹ Mean and standard deviation of numbers of flowers at different seasons.
² Statistics: *H* = Kruskal-Wallis nonparametric ANOVA; *U*_s = Mann-Whitney test, n.s. = *P* > 0.05; * = *P* ≤ 0.05; ** = *P* ≤ 0.01.

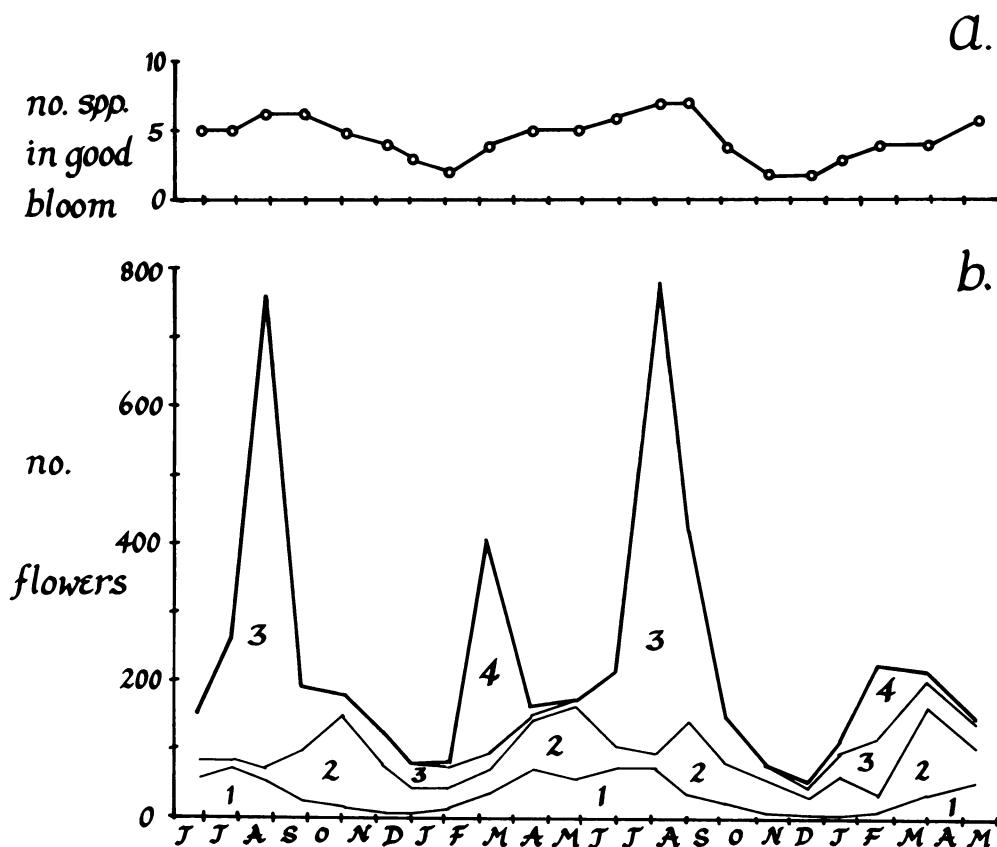


FIG. 9. Numbers of hermit (*Phaethornis guy*) foodplants in good bloom throughout the study period. 1 = *Heliconia* spp., *Costus* spp.; 2 = several dicot foodplants (Gesneriaceae, Labiatae, Malvaceae, Rubiaceae); 3 = *Razisea spicata*; 4 = *Columnea macrophylla*.

Were *H. jacula* the pollinator of *Marcgravia* spp., this would appear to be a fine example of bird-flower coevolution. In reality, the hummingbird is essentially a nectar-thief that seems to have organized its annual cycle at La Montura around such parasitism.

A variety of other flowers was visited, and in some cases pollinated, by *H. jacula* at La Montura. These were of secondary importance until *Marcgravia* flowers became scarce; then *H. jacula* often visited flowering trees (e.g., *Inga*, *Calliandra*), and sometimes defended territories at the abundant flowers of *Cephaelis elata* and (off the study area) *Heliconia latispatha*.

"Generalized" subcommunity.—As suggested above, this subcommunity represents something of a catch-all for small- to medium-sized hummingbirds, and flowers with short to medium-length corollas. No exclusive bird-flower associations are evident within this loose assemblage, in which flower choice by the birds more often reflects such factors as microhabitat preferences and aggressiveness. The number of hummingbird-pollinated flowers in good bloom in this subcommunity fluctuates irregularly during most of the year; few species were in good bloom in August–September 1980 or in October 1981. A somewhat different picture emerges if number of flowers is considered, since three species (the epiphytes *Cavendishia quereme* and *Thibaudia costaricensis*, and the treelet *Cephaelis elata*) produce many more flowers than the rest. The first two of these, along with *Columnea querceti* and two other species of *Cavendishia*, provided a rich supply of flowers in the forest canopy from about December through April (Fig. 11). This included the peak of the breeding season and at least the start of molt for *L. hemileucus*, *E. nigriventris*, *E. cupreiceps*, and *C. delphinae*. For these species, breeding was closely correlated with the abundance of flowers of these canopy epiphytes (Table 3). Blooming of these epiphytes tended to be uniformly distributed (but usually not significantly

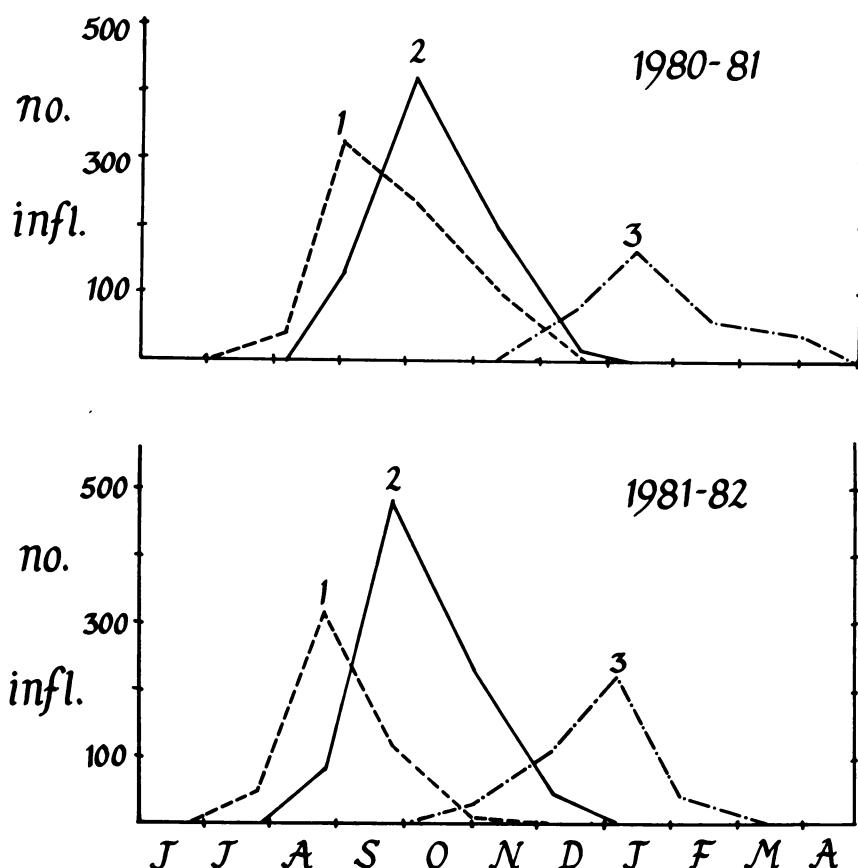


FIG. 10. Numbers of inflorescences recorded on three *Marcgravia* species used by *H. jacula*, 1980–1982. 1 = *M. schippii*; 2 = *M. affinis*; 3 = *M. pittieri*. Each inflorescence is subtended by one nectar-bearing bract.

so) during the birds' breeding seasons (Table 5). Annual variations in timing of breeding in these hummingbirds corresponded rather well with annual variations in timing of flowering, in particular the attainment of good bloom by *C. capitulata*, which occurred about a month earlier in 1980–1981. On the other hand, in both years *E. nigriventris*, *C. delphinae*, and to a lesser extent *E. cupreiceps* left the community during much of the flowering period of *Cephaelis*. This coincided approximately with an influx of *T. colombica*, *C. hemileucurus*, and *C. thalassinus*, and largely explains the negative correlation between the abundance of these two groups (Table 3).

A final group of flowers that is best discussed here includes those species that are visited, but not pollinated (at least not exclusively) by various species of hummingbirds. These species have mostly short-tubed or cup-shaped corollas or nectar-bracts; their often very abundant flowers generally produce little nectar. Included are several trees, especially of the Mimosaceae (*Inga* spp., *Pithecellobium arboreum*, and especially *Calliandra arborea*), two species of Marcgraviaceae (*Norantea sessilis*, *Souroubea* sp.), and a variety of other epiphytes (e.g., *Clusi*a spp.), shrubs (e.g., *Palicourea* spp., *Witheringia warsewiczii*), and lianas (Bignoniaceae, Compositae, Apocynaceae) (Appendix I). For most species of La Montura hummingbirds, these flowers are "supplementary," visited primarily when preferred, usually ornithophilous flowers are scarce or unavailable (due to defense by other, more aggressive hummingbirds). However, two hummingbird species seem to be more regularly associated with such plants (and are thus somewhat peripheral in terms of the community of hummingbird-pollinated plants *per se*): the fairly large *C. delphinae*, and the small *D. conversii*. The most important plant of this

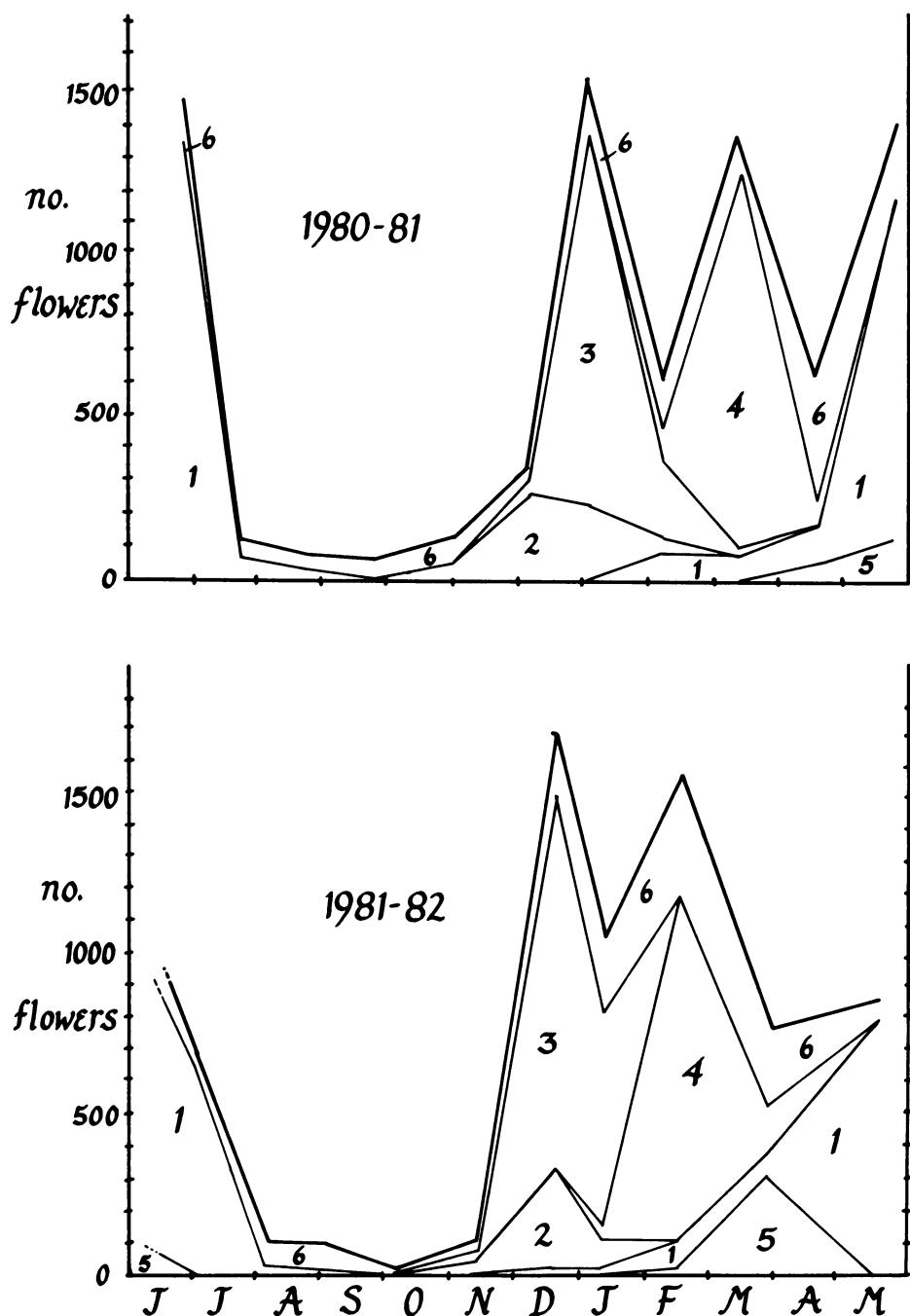


FIG. 11. Numbers of flowers recorded on foodplants used by hummingbirds of the generalized sub-community throughout the study period. 1 = *Cephaelis elata*; 2 = *Cavendishia capitulata*; 3 = *C. quereme*; 4 = *Thibaudia costaricensis*; 5 = *C. endresii*; 6 = other species (Rubiaceae, Cucurbitaceae, Gesneriaceae, etc.).

group for the hummingbird community as a whole is undoubtedly *Calliandra arborea* because of its abundance and year-round blooming (albeit with a pronounced peak around June–July). Probably pollinated mainly by sphingids or small bats, this tree is also a mainstay of the nectar-robbing Bananaquit.

DISCUSSION

SEASONAL ASPECTS OF HUMMINGBIRD-FLOWER INTERACTIONS

The relationship between plant-pollinator interactions and flowering seasons of the plants has been the subject of much recent controversy (see review in Feinsinger 1983). The observed dispersion of flowering seasons of plants sharing pollen vectors has often been considered to result (at least in part) from competition for pollinator services (e.g., Macior 1971; Frankie et al. 1974; Heithaus 1974; Stiles 1977), although specific tests of this hypothesis are few (Waser 1978a, b). This interpretation has been challenged on the basis that competition for pollinators should produce uniform spacing of blooming peaks, yet the blooming peaks of several such sets of plants show dispersions that are statistically random or even aggregated (Poole and Rathcke 1979). However, the validity of these tests rests upon the biological appropriateness of assuming that all times within the analysis interval are equal with respect to (a) the physiological capacities for flowering by the plants, and (b) the demand for plant rewards (in this case, nectar) by the pollinators. Elsewhere I argued against the validity of the first assumption (Stiles 1979b); here I address the second.

A number of investigations have concluded that hummingbirds breed when flowers are most abundant (Skutch 1950; Snow and Snow 1964; Stiles 1980), but the relation between flowering phenology and nectar demand has yet to be examined quantitatively. Available data and calculations suggest that the energy requirements of a hummingbird population will at least double in the course of the breeding season (Calder 1974; Ricklefs 1974). Molt might easily increase the daily energy requirements of an individual by up to 30% (King 1980). Thus, the nectar demand of a hummingbird population should rise through the breeding season (reflecting increased energy demands of adults, growth requirements of the young, and ultimately the population increment). If molt follows breeding directly, nectar requirements will remain high for several weeks or months, before declining to maintenance levels. From the flowers' point of view, competition for pollinators should be relaxed at this time due to higher pollinator availability, which should result in reduced selection for divergence in blooming seasons. Even in the simplest case of a single sedentary hummingbird interacting with a limited and exclusive set of flower species, one would not expect a uniform distribution of flowers through the year if the bird's reproduction were at all seasonal. Rather, there should be a predictable (from the bird's point of view) season of higher nectar availability—more flowers, more species of flowers, and/or more nectar-rich flowers—corresponding to the period of high energy demands of the bird. Within this period there might well be competition for the pollinator's services—but at a different level from the rest of the year. Taking the entire year as the unit of phenological analysis may therefore lead to misinterpretation of the significance of competition for pollinators in determining the spacing of blooming seasons.

A case in point is my conclusion that the dispersion of the blooming peaks of hermit (*Phaethornis superciliosus*)-pollinated flowers at Finca La Selva reflected possible competition for the services of this pollen vector (Stiles 1977). This conclusion was criticized by Poole and Rathcke (1979) as mentioned above. Actually, there were two broad peaks of flower availability, in the dry and early wet seasons. These two periods were separated by a period of lower (but still high) flower availability during the dry-wet transition, which I argued (1979) was a physiologically unfavorable time for flowering for most plants. However, the two clusters of blooming peaks correspond to the peak of breeding of *P. superciliosus*, and the end of breeding and the peak of molt, respectively. Moreover, within each of these periods taken separately, blooming peaks are overdispersed (Cole 1981). Thus, the observed pattern is precisely what would be expected to result from competition for pollinators, if the physiology of the plants and the nectar demand of the pollinators were taken into account.

Population movements also affect the energy demands of an area's hummingbird community, either accentuating or cushioning the amplitude of variations in the demands of sedentary individuals and species. A very constant nectar demand by one or several species over the year will most likely reflect emigration during the breeding season, immigration in the non-breeding season, or both. Conversely, such movements may be an integral part of a

species' strategy for satisfying its energy requirements when the availability of rich nectar sources varies in space and time (Feinsinger 1980; Stiles 1980).

Many of these patterns are clearly reflected in the flowering of hummingbird foodplants at La Montura. The theoretical case of a single sedentary hummingbird with its limited, exclusive set of foodplants is rather closely approached by the Lancebill subcommunity. Superimposed upon a highly uniform distribution of flowering peaks is a period of higher flower abundance during which *D. ludovicae* breeds; intermediate flower availability prevails during molt. The lower flower abundance during molt, and the fivefold difference in this parameter between breeding and quiescent periods, evidently correspond to a partial postbreeding emigration.

The two members of the hermit subcommunity place different demands upon the study area's nectar resources. *E. aquila* varies in abundance with the flowering of *Centropogon*, but its energy demands for breeding and molt are apparently satisfied elsewhere. The phenologies of *P. guy* and its foodplants appear nearly as closely linked as in the Lancebill subcommunity. Blooming periods are not uniformly distributed over the entire year, but they tend toward uniform distributions within both breeding and quiescent periods considered separately. Peak flower availability corresponds with the period of molt-breeding overlap, and earlier in the breeding season flower availability averages twice that during late molt and quiescent periods. The specific association of breeding by *P. guy* and blooming of the high-nectar *Heliconia* flowers emphasizes the close ecological relationship that seems to exist between these two genera throughout their distributions (Stiles 1979a, 1981).

Such patterns are much less clearcut in the generalized subcommunity because of the number of species involved, the low degree of bird-plant specificity, and the manifest importance of population movements in the annual cycles of most of the hummingbird species. Certainly, periods of high flower availability on the one hand, and of high nectar demand (breeding and molt) by the pollinators on the other, generally correspond (Table 4). There are some suggestions of competitive interactions among certain foodplants, however. There was little or no overlap in blooming between the three really abundant plant species (*Cavendishia queremei*, *Thibaudia costaricensis*, *Cephaelis elata*). Blooming peaks of some rarer species may be "repulsed" by those of more abundant species, notably that of *Cavendishia endresii* by that of *Thibaudia*; as a result, the former may exhibit major changes in its blooming period from one year to the next. The almost complete separation of blooming periods of *Cavendishia capitulata* and *C. endresii* may reflect selection for genetic isolation, as these species are virtually identical in floral morphology. In general, however, specific interactions in this subcommunity are difficult to detect and more study is required, particularly with respect to the possible relation between the flowering of such canopy epiphytes, and hummingbird visitation of the various "supplementary" flowers of the area.

SEASONALITY IN OTHER HUMMINGBIRD-FLOWER COMMUNITIES

Seasonal activity patterns of birds and flowers have been studied in detail at two other Costa Rican sites: Finca La Selva, at 100 m in the Caribbean lowlands below La Montura (Stiles 1975, 1978, 1980; Stiles and Wolf 1979); and Cerro de la Muerte, at 3000 m on the crest of the Cordillera de Talamanca (Wolf 1969, 1976; Wolf and Stiles 1970; Colwell 1973; Wolf et al. 1976). In addition, Skutch (1950, 1966) discussed hummingbird breeding seasons in the El General Valley, at 650 m on the Pacific slope below Cerro de la Muerte, and fragmentary data are available for hummingbirds of the dry forests of Guanacaste, in northwestern Costa Rica (Stiles and Wolf 1970; Wolf 1970). Finally, Feinsinger (1976, 1977, 1978) carried out detailed studies of flowering and hummingbird foraging at Monteverde, at 1200 m on the Pacific face of the Cordillera de Tilarán in northern Costa Rica.

As at La Montura, primary habitats were emphasized in the La Selva study, but some secondary habitats were also included. The Cerro de la Muerte study was done in secondary habitats, but fairly extensive comparisons with primary forest were included. Both primary and secondary habitats were included in the Guanacaste and El General Valley studies, but the Monteverde work was done entirely in young second growth, in a transitional area between the major forest types of the region.

The hummingbird-flower community of La Selva is similar in size to that of La Montura (ca. 20 hummingbirds, 50 hummingbird-pollinated plants), but differs in composition: there are five resident hermit hummingbirds and eight to nine nonhermits, three regular seasonal visitors, and four rare to accidental species. Floristically, the hummingbird foodplants of the understory (many *Heliconia*, *Costus*, *Cephaelis elata*, *Besleria* spp.) are more similar to those

of La Montura than are those of the canopy (bromeliads dominant, Ericaceae insignificant). Cerro de la Muerte has a smaller community (ca. five hummingbirds pollinating 20 flower species) with no hermits; all five hummingbird species breed there, but three emigrate for part of the year. Species of Ericaceae are important foodplants in the canopy as at La Montura, but the understory is distinct in terms of hummingbird foodplants. Practically all hummingbird species at La Selva breed between about January and June, and molt between June and September; all groups of hummingbird foodplants show flowering peaks in March–April and July–August, with a pronounced flower scarcity in November–December. The only hummingbird species that apparently departs from this pattern is the nectar-robbing, highly insectivorous *H. barroti*, which breeds from July or August to at least October. Thus, breeding and molting activity at La Selva is at its nadir when most species at La Montura are attaining their peak of breeding; the molting seasons of the La Montura species coincide with the main breeding season at La Selva. Only *P. guy* at La Montura overlaps the La Selva species in its breeding season, which begins 1 to 3 months later than that of its lowland congener, *P. superciliosus* (Stiles 1980). In the El General Valley the hermits also tend to show a breeding peak around July–August, and most nonhermits around January in the dry season (Skutch 1950). On Cerro de la Muerte, the main breeding season is roughly September through about January or February, but there is considerable variation among species and between years. The abundant *Panterpe insignis* may begin to breed as early as May and may finish in October; *Colibri thalassinus* may not commence breeding until December. Flowering patterns vary greatly from year to year, and breeding seasons may do likewise (Wolf et al. 1976). The hummingbirds of the Guatemalan mountains resemble those of the Cerro de la Muerte in breeding mostly at the coldest and wettest time of year, roughly October to January, since flowers are most abundant at this time (Skutch 1950). On the Cerro de la Muerte, the relevant flowers are epiphytic Ericaceae (as at La Montura), as well as species of *Centropogon*, *Fuchsia*, and *Salvia*.

Although detailed data are lacking, most species of Guanacaste hummingbirds seem to breed during the dry season and molt during the early wet season (at least *Amazilia* spp.; cf. Stiles and Wolf 1970). The seasonal pattern thus somewhat resembles that at La Selva, but the flowers most important for the breeding of most Guanacaste hummingbirds are pollinated by other agents, notably large bees. Wolf (1970) interpreted this to mean that the hummingbirds are relatively recent invaders of a basically insect (and bat)-pollinated plant community. Unfortunately, too little information is available on breeding and molt of Monteverde hummingbirds to relate these events to flowering patterns, and movements into and out of Feinsinger's study areas evidently reflected in large part flowering in adjacent forest habitats. Nevertheless, he found that flowers were available on these areas year-round, and that at some seasons hummingbird numbers tracked flower abundance fairly closely (Feinsinger 1977, 1978).

SUBCOMMUNITIES IN OTHER HUMMINGBIRD-FLOWER COMMUNITIES

My principal criterion for dividing the La Montura hummingbird-flower community into subcommunities was the degree of overlap in flower use by the birds (Fig. 7). The resulting division is correlated with bill length and curvature, since these largely determine a hummingbird's ability to extract nectar from a given flower. However, I neither require nor necessarily expect that other aspects of morphology and behavior will sort out neatly along subcommunity lines. A very different way of subdividing hummingbird guilds, based precisely upon foraging tactics and attempting to draw detailed morphological correlations, was advanced by Feinsinger and Colwell (1978). These authors classified hummingbirds according to their "ecological roles," which were defined not only by the flowers visited, but even more by how they are visited—i.e., whether they are defended or traplined, etc. A detailed critique of this approach will be presented elsewhere; here I explain my reasons for considering the Feinsinger-Colwell scheme inappropriate for the aims of this paper.

My major disagreement with Feinsinger and Colwell concerns the extent to which particular "ecological roles" characterize particular hummingbird species under all, or even most circumstances. Consider *D. ludovicae*, morphologically a classical "high-reward trapliner" in their scheme, because of its specialized bill and flower visitation. While many individuals do indeed trapline small clumps of epiphyte flowers, many males consistently defend rich clumps of *Satyria* and *Cavendishia* sp., while other males and females attempt to poach. A "classical"

territorialist like male *L. hemileucus* may trapline flowers of low to high nectar content at any time of the year, or may mix such traplining with defense of rich clumps, even on a daily basis. Much the same could be said for most La Montura hummingbirds, especially in the "generalized" subcommunity. Even the traplining *P. guy* may show transient defense of large clumps of flowers against other hermits before moving on. This does not necessarily imply that "ecological roles" do not exist, but I think that they are applied more appropriately to sex-age groups or to individuals at particular times and at particular flowers, than to species in most cases—and to me, seasonal patterns are most meaningfully treated at the species level. Similarly, Feinsinger and Colwell considered large and small clumps of flowers within a given plant species as separate "resource states." This distinction is valid if foraging tactics are being considered, but it would only be useful for my purposes were blooming seasons to vary systematically with clump size. I have no evidence that this occurs in any plant species at La Montura. For all these reasons, I prefer to compare hummingbird-flower communities in terms of subcommunities rather than "ecological roles."

The division of the hummingbird-flower community into subcommunities is quite notable at La Selva. The hermit subcommunity is quite diverse and complex, with some members overlapping more with nonhermits in flower use than at La Montura. One member, *Threnetes ruckeri* pierces many flowers, and seems especially closely associated with those of the large-bee-pollinated genus *Calathea*. As at La Montura, *E. aquila* is rare and visits only one or two flower species; its center of distribution appears to be at ca. 300 to 600 m between the two sites. The hermit subcommunities of La Selva and La Montura resemble each other most closely in both taxonomic composition and seasonal behavior. The generalized subcommunity at La Selva resembles that of La Montura in consisting mainly of canopy species; the sharp difference in seasonality reflects the difference in blooming between dominant groups of canopy foodplants—the Bromeliaceae at La Selva, the Ericaceae at La Montura. This subcommunity at La Selva may be further subdivided into a group of small hummingbirds (2–3 g) and nectar-poor flowers, and a group of medium-sized (4–7 g) hummingbirds and flowers with longer corolla tubes and greater nectar flow. No real analogue of the *Heliodoxa-Marcgravia* association occurs at La Selva, and the only long-billed canopy specialist possibly analogous to *D. ludoviciae*, is the rare and perhaps nonresident *Heliomaster longirostris*.

On Cerro de la Muerte, with only four to five species, the possibilities for defining subcommunities are decidedly limited. Nevertheless, the long-billed *Eugenes fulgens* and its long-tubed flowers do form a subunit apart. Females in particular visit scattered shrubs in the forest understory, thus becoming hermit analogues; the males do this and also visit certain long-tubed canopy flowers (*Columnea magnifica*, *Passiflora* sp.) in the manner of lancebills. The remaining species comprise the "generalized" subcommunity, within which a great deal of foraging overlap is noted. The small (2.8 g) *Selasphorus flammula* shows a limited divergence from the others in that it visits relatively more small, low-nectar, short-corolla flowers, but even here it overlaps widely with the larger generalist *Panterpe insignis* (5–6 g). Like *E. nigriventris* and *E. cupreiceps* at La Montura, it scarcely merits separate subcommunity status.

Detailed foraging data are lacking for Guanacaste dry-forest hummingbirds, but most species appear to constitute a large generalized grouping. Only the long-billed *Heliomaster constantii* may be separable on the basis of its visits to some long-tubed flowers, but even this requires confirmation. Much the same might be said of the second-growth community at Monteverde studied by Feinsinger (1976, 1977, 1978). This community is far simpler than that of La Montura at a fairly similar elevation, containing only two "principal" hummingbird species and ca. five common seasonal visitors, that together visit some 10 to 15 flower species. Most hummingbirds overlap sufficiently at most plant species to render clearcut division of the community on this basis difficult.

Three subcommunity types thus recur with some regularity in the hummingbird-flower communities of humid tropical forests: (1) long-billed hummingbirds and long-tubed flowers of the forest canopy; (2) long, usually curve-billed hummingbirds and understory flowers with corresponding corollas; and (3) a large, generalized subcommunity of small- to medium-sized, straight-billed hummingbirds and flowers with straight, short- to medium-length corollas. In dry forests and young second growth, this may be the only subcommunity present. This subcommunity may be further divisible on the basis of hummingbird size and bill length, and flower length and nectar flow, along the lines suggested by Feinsinger and Colwell (1978) if values of overlap in flower visitation between the putative subgroups are sufficiently low.

Finally, extrinsic to these systems may be one or more nectar-robbing species like *H. barroti* (and *Coereba*) at La Montura, as well as species that parasitize other plant-pollinator systems, such as *H. jacula* at *Marcgravia* spp.

IS THE LA MONTURA HUMMINGBIRD-FLOWER COMMUNITY COEVOLVED?

This study has demonstrated a close correspondence between the annual cycles of some La Montura hummingbirds and the flowering phenology of their foodplants. To what extent is this mutualism truly a result of plant-pollinator coevolution? Janzen (1980) presented a rigorous definition of coevolution, emphasizing the repeated, reciprocal evolutionary responses of each partner to selective pressures generated by the other. He also described cases that mimic coevolution, in which one participant enters the system and takes advantage of the scarcity or absence of (or displaces) one coevolved partner, then interacts with the other in a manner suggestive of a coevolved relationship. Another complication occurs when one or both coevolved partners actually consists of groups of species; coevolutionary responses are then much more diffuse and difficult to distinguish from fortuitous relationships.

Indirect evidence must normally be used to distinguish the results of bona-fide coevolution from fortuitous, recently-derived associations. Such evidence could include the complexity, degree of obligateness (in the case of mutualisms), and exclusiveness of the interaction itself, with the more complex, exclusive, and obligate associations being more likely to be truly coevolved. The degrees of precision and efficiency are also likely to be greater in a coevolved mutualism than in a fortuitous one. Historical and biogeographic considerations also apply: is there evidence that one or both partners are recent invaders or at the edge of their distributions, or that other possible participants are now extinct? Do present distributions and ecology suggest that both parties to the interaction share a long period of evolution and adaptation in the same localities and habitats?

These criteria are satisfied to different degrees by the different subcommunities at La Montura. The complex, precise, and relatively exclusive correspondences between bills and corollas in the hermit and lancebill subcommunities are certainly suggestive of bona-fide coevolved relationships (although the degree of dependence of *E. aquila* on *Centropogon* flowers for energy resources for breeding and molt is nil, at least on the study area). The generalized subcommunity is clearly an example of diffuse coevolution at best, and some of its members (e.g., *C. delphinae*, *D. conversii*) may in fact be fortuitous associates. Certainly the annual cycles of *L. hemileucus*, *E. nigriventris*, and *E. cupreiceps* seem much more closely correlated with blooming patterns of the principal ornithophilous plants than are those of *C. delphinae* or *D. conversii*.

The *Heliodoxa jacula-Marcgravia* association is clearly not a mutualism, and probably is not coevolved at all. This hummingbird has organized its annual cycle about its parasitism of *Marcgravia*, but because its cycle does not deviate markedly from those of other straight-billed species, the association may not be more than facultative; *H. jacula* is certainly quite capable of visiting many other flowers on the study area. On the other hand, the inflorescence structure of *Marcgravia* seems to deter hummingbirds that cannot cling strongly to the nectar bract: the strong feet of *H. jacula* probably represent a preadaptation (perhaps even an adaptation) for overcoming this defense. Selection on *Marcgravia* to reduce or counteract parasitism by *H. jacula* may be weak because much nectar is secreted at night, and is thus available to pollinators; also, the timing of anthesis precludes direct interference with pollen flow by hummingbirds.

Seasonal patterns provide another way of assessing whether many bird-flower associations at La Montura are fortuitous or coevolved: do the principal events of the annual cycles of birds and flowers occur at the most favorable times in terms of other parameters, such as physiology (cf. Herrera 1982)? It is significant that the main breeding season of the birds, and the greatest flowering of ornithophilous plants occur during the coolest and wettest time of year; both end in the early dry season. For most plant groups and in most areas, heavy rainfall is decidedly unfavorable for flowering (reviews in Frankie et al. 1974; Stiles 1978). Heavy rainfall may also restrict the time available to hummingbirds for foraging, and thus diminish energy reserves for nesting females (Calder 1974; Foster 1974). On physiological grounds, nesting by the birds and flowering by the plants are both occurring at a relatively improbable time of year. The reason for this is not well understood, but may reflect a lower abundance of nectar-robbing insects at this time. Direct data on insect abundance are lacking, but it is noteworthy that nearly all insectivorous birds of La Montura breed in the late dry and early

wet seasons (Stiles, unpubl. data; cf. Skutch 1950). A further indication that this relationship is more than fortuitous is the fact that nearly all La Montura hummingbirds start to breed about a month *before* their respective flowers attain high levels of blooming; thus, the increase in flowering coincides closely with the period of rapid growth of nestlings in their first broods. This suggests a more intricate degree of coadaptation of timing mechanisms than simply having an abundance of flowers trigger breeding.

All of the major hummingbirds and flowers of the La Montura community seem to be characteristic components of primary subtropical forest ecosystems in Costa Rica (for plant distributions and ecology see Standley 1937–1938; Durkee 1978; Skog 1978; Wilbur and Luteyn 1978; Dwyer 1980; and Stiles 1982; for similar information on birds see Slud 1964; Ridgely 1975). Indeed, many of the birds and plants are endemic to the mountains of Costa Rica and Panama including the principal birds and flowers of the generalized subcommunity. The hummingbirds *E. aquila*, *D. ludovicae*, *D. conversii*, and *P. guy* reach their northern limits in Costa Rica, but well to the north of La Montura; all range south into South America, where their associations with flowers resemble those seen at La Montura (Snow and Snow 1972, 1980; B. A. Stein, pers. comm.). Thus, most species of birds and flowers of the La Montura community seem to share a long period of evolution and adaptation in the same region and habitats, thereby also satisfying this criterion for coevolved relationships.

Many bird-flower relationships of the primary forests of La Selva and Cerro de la Muerte probably also satisfy the requirements for being considered true coevolved mutualisms (cf. Wolf et al. 1976; Stiles 1978, 1980). The situation is far from clear in the second-growth communities studied by Feinsinger (1978). Although the second growth itself is obviously of recent anthropogenic origin, many of the plants and birds of such habitats are also characteristic of natural forest edge and light gaps, and may in fact have been associated for long periods (Stiles 1975). Determining the degree to which plant-pollinator patterns in secondary vegetation reflect fortuitous accidents or historical associations will certainly require extensive studies in the original primary habitats of the region (Wolf et al. 1976; Feinsinger 1983). This represents one more argument for the preservation of primary forest, in order to better understand the second-growth vegetation with which man is so rapidly replacing it.

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APPENDIX I
HUMMINGBIRD FOODPLANTS OF LA MONTURA

	Growth habit ¹	Bloom. seas. ²	Corolla length ³	Corolla curv. ⁴	Nectar prod.	Coloration ⁵	Max. abund.	Visitors ⁶
A. Hummingbird-pollinated species								
<i>Heliconia deflexa</i> (Musaceae)	H	A ₁	37	M	H	yellow + green, red ¹	10	Pg
<i>H. ignescens</i> (Musaceae)	H	A ₁	35	M	H	yellow, red-orange ¹	32	Pg
<i>H. mathiasae</i> (Musaceae)	H	B ₁	34	S	H	yellow + red, red ¹	6	Pg
<i>H. rodriguezii</i> (Musaceae)	H	B ₁	35	M	H	yellow, red ¹	52	Pg
<i>H. trichocarpa</i> (Musaceae)	H	A ₁	33	M	H	yellow, red ¹	18	Pg, Ea
<i>H. arorpurpurea</i> (Musaceae)	H	A ₁	32	S-M	H	white, red ¹	4	Pg
<i>Costus pulverulentus</i> (Zingiberaceae)	H	A ₁	42	S	H	red, red ¹	29	Pg
C. sp. (Zingiberaceae)	H	A ₁	30	S	H	yellow, red-orange ¹	10	Pg, Hj
<i>Renalmia cernua</i> (Zingiberaceae)	H	A ₁	14	O-S	L	orange, orange ¹	7	Lh, En, Ec, Tf
<i>Alpinia</i> sp. (Zingiberaceae)	H	A ₁	28	S	H	white, red ¹	27	Pg, Hj
<i>Guzmania lingulata</i> (Bromeliaceae)	E	D	40	O	—	yellow, red ¹	5	Dl, Lh
<i>G. donnell-smithii</i> (Bromeliaceae)	E	D	32	O	H	white, red ¹	7	Dl, Lh
<i>G. plicatifolia</i> (Bromeliaceae)	E	B ₁ ?	22	O	—	yellow, orange ¹	13	Lh, Hj, Dl
<i>G. coryostachya</i> (Bromeliaceae)	E	B ₂	16	O	—	white, green ¹	16	Lh, Hj, Dl
<i>G.</i> sp. (Bromeliaceae)	E	D	27	O	L?	yellow, red ¹	55	Dl, Lh, Hj
<i>G. aff. scherzeriana</i> (Bromeliaceae)	E	D	16	O	—	orange, green ¹	7	Lh, Dl, Hj
<i>Pitcairnia valerii</i> (Bromeliaceae)	E	A ₁	8	O	—	red, green ¹	8	Lh, Ec, En
<i>Elleanthus aurantiacum</i> (Orchidaceae)	E	A ₁	ca. 5	O	L	orange	13i	Lh, En, Ec
E. sp. (Orchidaceae)	E	A ₁	ca. 5	O	—	purple	15i	Lh, En, Ec
<i>Spiranthes</i> sp. (Orchidaceae)	H	A ₁	36	O-S	—	red	4	Pg
<i>Pstittacanthus rodosus</i> (Loranthaceae)	E	B ₂	28	O	—	yellow + orange	180	Dl, Hj
<i>Malavaviscus arboreus</i> (Malvaceae)	S	C	38	O	H	red	26	Pg; others pierce
<i>Cephaelis elata</i> (Rubiaceae)	B ₁	11	O	L	white, red ¹	1350	Lh, En, Ec, Ch, Tf, Hj, Lc	
<i>Ravnia triflora</i> (Rubiaceae)	E	A ₁	43	S	—	red	21	Pg
<i>R. pitieri</i> (Rubiaceae)	E	A ₁	41	S	—	red-orange	5	Pg
<i>Aphelandra tridentata</i> (Acanthaceae)	S	A ₁	31	S	—	red	15	Pg
<i>Razisea spicata</i> (Acanthaceae)	S	B ₁	40	S	H?	orange + yellow	685	Pg; others pierce
<i>Scutellaria costaricensis</i> (Labiatae)	S	C	40	S	H	red + yellow	60	Pg; others pierce
<i>Centropogon granulosus</i> (Lobeliaceae)	S	C	34	V	H	red	95	Ea, Pg
<i>Alloplectus tetragonus</i> (Gesneriaceae)	S	A ₂	40	S	H	orange	51	Pg
<i>Besleria solanoides</i> (Gesneriaceae)	S	B ₂	15	O	L	orange	72	Ec, En, Lh
<i>B. notabilis</i> (Gesneriaceae)	S	A ₁	14	O	L	orange	90	Ec, En, Ct
<i>B. laxiflora</i> (Gesneriaceae)	S	B ₂	13	O	—	orange	34	Ec
<i>Colomnea purpureata</i> (Gesneriaceae)	E	A ₂	25	O-S	H	yellow, orange ²	15	Lh, Lc, En
<i>C. macrophylla</i> (Gesneriaceae)	E	A ₁	33	S	L	orange	310	Pg
<i>C. quereti</i> (Gesneriaceae)	E	A ₁	15	S	L	red + yellow	392	Lh, En, Cd

APPENDIX I
CONTINUED

	Growth habit ¹	Bloom. seas. ²	Corolla length ³	Corolla curv. ⁴	Nectar prod. ⁵	Coloration ⁶	Max. abund. ⁷	Visitors ⁸
<i>C. consanguinea</i> (Gesneriaceae)	E	D?	18	O-S	L	yellow	14	Lh, En
<i>Drymonia conchocalyx</i> (Gesneriaceae)	S-T	D?	28	O-S	—	purple	22	Hj
<i>Cavendishia capitulata</i> (Ericaceae)	E	A ₁	12	O	L	purple + white, pink ¹	250	Lh, En, Ec
<i>C. quereme</i> (Ericaceae)	E	A ₁	11	O	L	orange + white, pink ¹	1320	Lh, En, Ec
<i>C. endresii</i> (Ericaceae)	E	A ₁	12	O	L	purple + white, pink ¹	361	Lh, En, Ec
<i>C. callistis</i> (Ericaceae)	E	A ₁	32	O	—	white, pink ¹	92	Dl, Hj
C. sp. (Ericaceae)	E	A ₁	30	O	—	pink + white, pink ¹	327	Dl
<i>Satyrivia warsewiczii</i> (Ericaceae)	E	A ₂	31	O	H	red + white	295	Dl
<i>Thibaudia costaricensis</i> (Ericaceae)	E	A ₁	10	O	L	white, pink ¹	1200	Lh, En, Ec, Cd
<i>Pstammisia ramiflora</i> (Ericaceae)	E	A ₁	27	O	H	red + white	145	Dl, Pg, Lh
<i>Gurania costaricensis</i> (Curcurbitaceae)	V	D	7	O	—	yellow, orange ¹	21	Ec, En, Lh, (Pg)
<i>G. leyana</i> (Curcurbitaceae)	V	D	9/17	O	L	yellow, orange ¹	10	Ec, En, Lh
G. sp. (Curcurbitaceae)	V	D	—	O	—	yellow, orange ¹	7	Ec, En, Lh
<i>Sympomonia globulifera</i> (Guttiiferae)	T	A ₁	10±	O	—	red	ca. 1000	Cd, Lh, En
<i>Erythrina lanceolata</i> (Fabaceae)	T	A ₁	28	H	—	red	26	Pg, (Dl?)
B. Species frequently visited by hummingbirds, but pollinated mostly by other agents								
<i>Palicourea lasiorrhachis</i> (Rubiaceae)	S	A ₁	10	O	L	yellow	150	Lh, En, Ec
P. sp. (Rubiaceae)	S	A ₁	6	O	L	green	70	En, Ec
<i>Coussarea</i> sp. (Rubiaceae)	S-T	A ₁	20+	O-S	—	white	580	En, Ec, Pl (pierce)
<i>Marcgravia schippii</i> (Marcgraviaceae)	E	A ₁	ca. 20	O-S	—	brown, green ¹	335	Hj
<i>M. pittieri</i> (Marcgraviaceae)	E	A ₁	ca. 15	O	—	brown, green ¹	215	Hj
<i>M. affinis</i> (Marcgraviaceae)	E	A ₁	ca. 12	O	—	brown, green ¹	550	Hj, Lh
<i>Noranthea sessilis</i> (Marcgraviaceae)	E	A ₁	5	O	—	red, brown ¹	70i	Cd, En, Ec, Lh, Pg
<i>Clusia</i> spp. (Guttiferae)	E	(A ₁)	3-6	O	—	white to cream	300+	Cd, En, Ec, Lh, Pg
<i>Inga</i> spp. (Mimosaceae)	T	(A ₁)	8-14	O	L?	white	3000+	Cd, Lh, En
<i>Calliantha arborea</i> (Mimosaceae)	T	C	12	O	L	pink, white	5000+	Cd, Lh, En, Ec, Pg, Ct
<i>Witheringia warsewiczii</i> (Solanaceae)	S	C	5	O	L	yellowish	350	Ec, En, Lh
<i>Hampaea appendiculata</i> (Tiliaceae)	T	A ₁	8	O	L?	whitish-yellow	ca. 200	En, Loh, Ec

¹ Growth habit: H = terrestrial herb; S = shrub; T = tree; E = epiphyte or hemiepiphyte; V = vine.

² Blooming Seasonality: A₁ = one discrete peak of flowering per year; A₂ = 2 discrete peaks per year (may vary in intensity). B₁ = population blooms fairly continuously, 1 well-defined peak per year; B₂ = population blooms irregularly but 1 well-defined peak per year; C = population blooms fairly continuously, with irregular and variable peaks; D = irregular bursts of flowering (discrete), much variation between years.

³ Corolla length: effective corolla length; corolla opening to nectar chamber.

⁴ Corolla curvature: same symbols as for bill curvature, Table 1.

⁵ Nectar production: H ≥ 20 µl/flower/day; L < 20 µl.

⁶ Color: color given is for corolla, except 1 = bract or inflorescence; 2 = calyx.

⁷ Max. abundance: high count in flower censuses (at peak bloom); i = number of inflorescences (many small flowers per inflorescence, not possible to count).

⁸ Principal visitors: according to abbreviations, Table 1, approximately in order of importance; species italicized accounted for 80% or more of observed visits.