

## ORGANIZATION OF A TROPICAL GUILD OF NECTARIVOROUS BIRDS<sup>1</sup>

PETER FEINSINGER<sup>2</sup>

*Section of Ecology and Systematics, and Department of Entomology,  
Cornell University, Ithaca, New York 14850 USA*

**Abstract.** Fourteen months' observations on hummingbird foraging patterns in successional habitats at Monteverde, Costa Rica, showed that one territorial species (*Amazilia saucerottei*) dominated rich resource clumps, modified all other species' patterns, and thus organized the nectarivorous bird guild. The principal nonterritorial species (*Chlorostilbon canivetii*), which *Amazilia* usually excluded from rich resources, traplined dispersed flowers and interfered with foraging patterns of other nonterritorial species. The 12 additional hummingbird species that foraged in the study habitats included species important in nearby communities, specialists on particular resources, and highly migratory opportunists.

Foraging patterns diverged along several dimensions, including (1) the species or flower density of the individual plant; (2) the strata of flowers within the plant; and, since nectar was renewed at variable rates, (3) the time of day. Analysis of foraging patterns along these dimensions required that a hierarchy of niche breadth and overlap measures be defined and contrasted. Patterns compared over an entire year showed that the two principal species exploited the broadest niches, but overlapped only 17%. In no case did overall foraging patterns overlap more than 21%, and overlaps between many approached zero. These values, however, did not reveal the degree of exclusion from resources that were potentially exploitable, or the intensity of competition.

Statistical correlations showed that most month-to-month changes in niche breadth, niche overlap, and population size could be attributed to shifts in the resource base. Of the 16 plant species exploited by hummingbirds, the forb *Lobelia laxiflora* and the tree *Inga brenesii* were responsible for most fluctuations in resource levels. Flowering peaks of both species attracted large numbers of hummingbirds; in general, numbers and diversity of hummingbirds rose with increased flower abundance rather than increased flower diversity. *Lobelia* nectar was effectively superabundant, and niche overlap during *Lobelia* peaks was high. Birds foraging in *Inga* trees, however, could diverge along spatial and diurnal dimensions, and overlap during *Inga* peaks was much lower. In between *Lobelia* and *Inga* peaks, the two principal hummingbird species usually dominated the guild, and expanded their niches but overlapped little. Each hummingbird species responded to that particular pattern of resource states it could best exploit, and the guild as a whole tracked the entire resource base. The cycle of resource flushes entrained these patterns to an annual rhythm.

**Key words:** Competition; Costa Rica; foraging strategies; guild; hummingbirds; niche breadth; niche overlap; pollinator behavior; resource partitioning; species diversity; territoriality; tropics.

### INTRODUCTION

Most tropical hummingbirds overlap extensively in the flowers they can exploit and compete belligerently for the nectar and arthropod contents of these flowers (see Stiles and Wolf 1970, Wolf 1970, Colwell 1973). Others have elongated or deeply curved bills which permit them to tap nectar from flowers that species with less specialized bills cannot reach (see Snow and Snow 1972, Stiles 1975). The transitory nature of secondary habitats at Monteverde, Costa Rica has apparently prohibited such coevolution between particular flowers and particular beaks, for most flowers in these habitats have corollas of such generalized shape that even the shortest-billed

hummingbird present can extract nectar from any flower that other hummingbirds visit. I wished to determine if these species nevertheless foraged in distinct patterns such that the ever-changing nectar resources were partitioned among them in consistent fashion.

Hummingbirds and other nectar-feeding birds exploit a common resource base in similar fashion and thus constitute a "guild" (Root 1967). The spectrum of food resources actually exploited by each population within the guild of a particular community is a dimension of that population's realized or actual niche (Colwell and Futuyma 1971, Whitaker et al. 1973). Given data on resource exploitation patterns, one can determine the actual niche breadth of each population, and the overlap between populations, along the diet axis. Shifts in these values should reflect important aspects of the guild's organization. Results can be compared with those of

<sup>1</sup> Manuscript received 11 February 1975; accepted 16 December 1975.

<sup>2</sup> Present address: Department of Zoology, University of Florida, Gainesville, Florida 32611 USA.

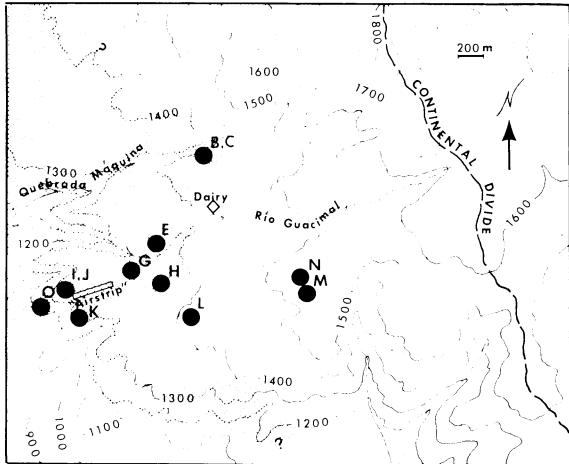


FIG. 1. Region of Monteverde, Costa Rica. Contour intervals in meters. Monteverde bench in center; stippled area is approximate extent of Lower Montane Moist Forest-Wet Forest Transition Zone. Letters denote study plots.

many resource partitioning studies (see reviews in Miller 1967, Pianka 1973, Schoener 1974a, Colwell and Fuentes 1975). The nectarivore-flower relationship permits relatively objective measures of resource use and resource availability, and a tropical environment that lacks physical extremes permits data-gathering over a full annual cycle. Thus, I could investigate the nectarivorous bird guild at Monteverde by measuring food resource abundance and diversity, and observing each hummingbird population's resource exploitation pattern, over 14 consecutive months.

#### STUDY AREAS

Monteverde is a small dairy-farming community located between 1,320 m and 1,540 m on a Pacific-facing bench of the Cordillera de Tilarán in northwest Costa Rica. Deep valleys to the south and west, and the continental divide to the northeast, delimit the bench (Fig. 1). From mid-May through late October, rains occur nearly every afternoon, as in other parts of Pacific Costa Rica. During the November-May trade wind season, however, the mountain barrier creates a rain shadow. While rain forests cover the Caribbean slope of the cordillera (Tosi 1969), lowland Guanacaste, to the west of Monteverde, experiences a severe dry season (Janzen 1967a, Wolf 1970, Holdridge et al. 1971). At Monteverde, the trade winds carry considerable mist over the divide, minimizing dry-season stress just west of the crest and allowing a typical Lower Montane Rain Forest to exist (Tosi 1969, see Holdridge 1967, Holdridge et al. 1971). But this mist dissipates quickly with distance, so that habitats farther west and down-slope experience increasingly severe dry seasons.

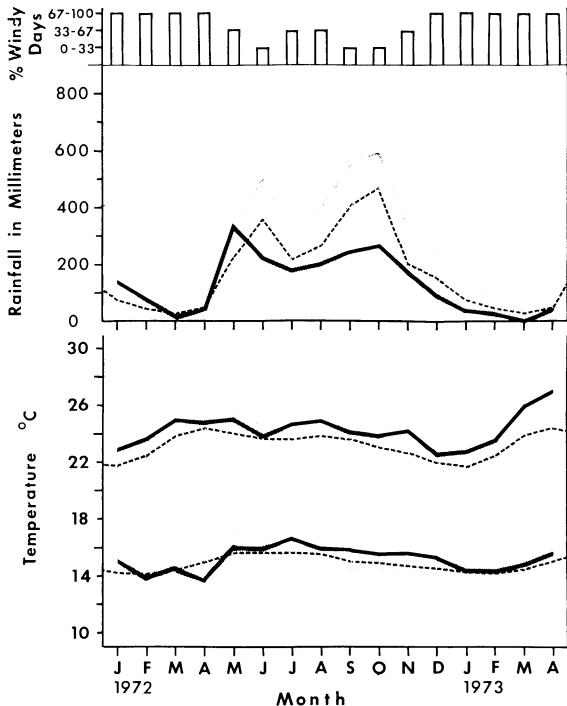


FIG. 2. Climate of the transition zone. Data collected at 1,370 m, near Plot E in Fig. 1. Mean monthly rainfall, mean daily maximum and minimum temperatures, and mean percent of days per month (1956-1971 inclusive) with wind sufficient to keep small limbs in motion. Dashed line and stippled area = monthly mean  $\pm$  one standard deviation (1956-1971 inclusive); solid line = January 1972-April 1973.

The region scarcely 2 km west of the divide, at 1,200-1,400 m, receives little precipitation during windy months (Fig. 2). This "life zone," the Lower Montane Moist Forest-Wet Forest Transition (Holdridge 1967, and G. V. N. Powell, *personal communication*), hereafter termed the "transition zone," extends horizontally across the Pacific face of the Cordillera de Tilarán and adjacent ranges (Tosi 1969, P. Feinsinger, *personal observations*). It is an ecotone between the lowland Pacific dry forests and the mesic montane and premontane forests extending over the divide and down the Caribbean slope. At Monteverde, and apparently throughout much of this zone, most untilled areas support abandoned or unimproved fields in various successional stages, including second-growth scrub mixed with secondary trees. Mature forest remains only between pastures and in ravines. Natural landslides and treefalls provide further openings. Abundant Chorotega American artifacts indicate that the transition zone has supported humans at least on a seasonal basis for many centuries. Thus periodic disturbance provides opportunities for successional species today and presumably has done so for some time.

I selected eight successional sites in this transition zone (B, C, E, G, I, J, K, and O of Fig. 1) for intensive study. Plots B, C, E, and G sampled representative mixed scrub and secondary trees along pasture edges and in abandoned fields at elevations of 1,370–1,400 m. Canopy closure in these communities was never complete; trees were often very dispersed. The herb-small shrub layer generally reached 1–2 m, while large shrubs and trees ranged from 5 to 15 m in height. Few trees or shrubs dropped their leaves during the dry season, but many herbs died back. The onset of rains in May initiated a noticeable flush of vegetative growth. *Inga brenesii* (Leguminosae) dominated the trees and large shrubs on all four sites, while *Cecropia obtusifolia* (Moraceae) and *Saurauia* sp. (Actinidiaceae) occurred regularly. "Guayaba," *Psidium guajava* (Myrtaceae), infested Plot C but rarely occurred on other plots. The herb-small shrub layer included many species of *Solanum* (Solanaceae) on all plots, as well as many species of Compositae, *Asclepias curassavica* (Asclepiadaceae), and *Rubus* spp. (Rosaceae).

Plot I was in virtually treeless mixed scrub 1.5–4 m high on an abandoned pasture at 1,320 m. This floristically diverse area typified many abandoned unimproved pastures in the Monteverde transition zone. *Eupatorium* sp. and *Vernonia triplosculosa* (Compositae), the most common shrubs, lost their leaves during the dry season, creating a marked visual contrast between dry and wet seasons. Plot I also contained most shrubs and herbs of Plots B, C, E, and G, plus many *Hamelia patens* (Rubiaceae). Many vines climbed over the scrub.

Plots J and K, in mixed scrub with scattered secondary trees at 1,320 m, included most species of Plot I but also contained several tree species of Plots B, C, E, and G. Physiognomy resembled that of the latter four plots, but scrub height varied from 0.5 to 1.5 m only. *Inga brenesii* and *Cecropia obtusifolia* were conspicuous. In addition, both plots contained *Inga* sp. 2. The epiphyte *Psittacanthus lateriflorus* (Loranthaceae) grew on scattered trees in Plot J.

Plot O, at 1,220 m, lay in the bean fields that covered many steep, drier slopes just below the shelf-edge. Though a few *Inga* sp. 2 remained in these fields, hand-clearing every October eliminated other large shrubs and trees. Thus, herbs such as *Lobelia laxiflora* dominated these fields. Like other plots, Plot O also contained *Asclepias curassavica* and many Compositae.

More mesic Monteverde habitats contained strikingly different vegetation. *Heliconia* sp. (Musaceae) and *Costus scaber* (Zingiberaceae) dominated the hummingbird-visited plant group in the understory of mature transition-zone forest (Plot H) at 1,380 m, whose physiognomy resembled that of Lower Montane Wet Forest (Sawyer and Lindsey 1971). Aban-

doned pastures in the Lower Montane Wet Forest above 1,400 m (Plot L) contained more mesic, evergreen plant species than the study plots. Acanthaceae, including at least five hummingbird-visited species, dominated the understory of mature forest above 1,520 m (Plots M, N) in the Lower Montane Wet Forest-Rain Forest Transition Zone. The abundant epiphytes also included several hummingbird-pollinated species.

Voucher specimens of the plants named above are deposited with the Field Museum (hummingbird-exploited species only), the herbarium of the Universidad de Costa Rica, and the Museo Nacional de Costa Rica in San José. A more complete list of plant species occurring on all plots is available from the author.

#### FIELD PROCEDURE

During November–December 1971, I investigated a variety of successional habitats in the transition zone and then laid out 1,470 m of transects: 800 m in mixed pasture-edge trees and scrub at 1,370–1,400 m elevation (Plots B, C, E, G), 260 m in secondary scrub at 1,320 m (Plot I); 290 m in mixed scrub and secondary trees at 1,320 m (Plots J, K); and 120 m in unimproved bean fields at 1,220–1,240 m (Plot O). I believed that the distribution of flora among these plots provided an accurate index to the relative abundance of hummingbird-exploited plant species in all successional transition-zone habitats. Studies were concentrated within these successional areas rather than mature forest not only because observation was difficult in the forest, where many hummingbirds exploited epiphytes, but also because hummingbirds appeared to treat the successional transition-zone habitats as a distinct unit. For comparative purposes, however, I also set up plots in other Monteverde habitats: 160 m in mature transition-zone forest (Plot H); 60 m in abandoned wet-forest pasture (Plot L); and 195 m in mature wet forest-rain forest transition (Plots M, N).

From January 1972 through April 1973 I worked in 1-mo blocks. At the end of each month the hummingbirds and flowering plants were censused along a 20-m-wide strip bisected by each transect. On each of three consecutive mornings, I visited one third of these transects. Beginning at daybreak, I spent 5 min on each 10–20-m-long transect segment, identifying to species each hummingbird that I encountered and noting the individual identity of any marked birds. Thus, each segment was censused at the same sun-time each month. Total time spent in hummingbird censuses was 144.5 h. In the afternoon of each census day, I noted all plant species in flower on each segment and collected any plant species not previously identified. I counted the number of flowers on plants of all hummingbird-exploited spe-

cies. When these flowers were so numerous that a direct count was impractical, I counted by tens or hundreds, correcting these estimates by first estimating, then counting the flowers of a subsample. All remaining monthly activities were restricted to these study habitats (Plots B, C, E, G, I, J, K, O). Census data from Plots H, L, M, and N are useful for comparative purposes but are not included in the numerical analysis below.

I spent a total of 260 h mist-netting hummingbirds, accumulating 1,576 net-hours. Weather conditions permitting, I netted from dawn to 1100 or 1200 on 2 days each in Plots B-C and I-J each month, and for 2 days each month March-May 1972 in Plot O. I weighed each hummingbird caught to 0.01 gm on a triple-beam balance, then measured to 0.5 mm the length of tail, wing chord, and culmen from base (see Baldwin et al. 1931). (Ornithologists usually measure length of exposed culmen; however, length of culmen from base more closely estimates the corolla length most efficiently exploited by a hummingbird.) I recorded sex (if possible) and age of the bird; deep striations in the culmen denoted immatures (Ortiz-Crespo 1972). Finally, each bird was color-marked following the method of Stiles and Wolf (1973). Each received a colored acetate leg-tag additionally coded with two strips of plastic tape and secured with Duco® cement. Each individual of a given species received a unique color combination. I also marked the bird's back with two dots of Pactra™ enamel paint corresponding to the plastic tape colors on the leg-tag. Recaptured birds were weighed, and retagged as necessary.

I spent 1,166 h observing hummingbird activity at flowering plants in the study habitats, chiefly at Plots B, C, I, J, K, and O. Each month I selected for observation a representative plant or plant clump of each potentially hummingbird-visited species then in flower. At flowering peaks of certain species, some individual plants or clumps held such high numbers of flowers that hummingbird foraging patterns at these flowers differed substantially from patterns observed at lesser flower densities. At these times, both a representative low flower density and a representative high flower density of that species were selected. Most plant species never reached such flower densities and required only one observation period per species per month. I occasionally made replicate observations during the month; at other times I observed plants of two species simultaneously.

During January and February 1972, onset and length of observation periods were not standardized. Data from the 152 observation hours accumulated during those months are useful from a comparative standpoint but were not analyzed. From March 1972 on, I standardized the time at which I began and

ended observation periods as much as possible. During the May–October rainy season, each period began at 0500 (May–June) or 0515 (July–October) and lasted for the next 7 h. In the dry season (March–April 1972, November 1972–April 1973), periods at plants visited frequently by two or more hummingbird species began at daybreak (0530 or 0545) and covered the full 12-h day. If visits were infrequent or limited to one bird species, observations were terminated after 8 h, or after 6 h if no hummingbirds came at all. (I converted data from observation periods < 12 h to a 12-h base by multiplying with the appropriate ratio, 12/8 or 12/7. This may have overestimated some figures for wet-season months, as hummingbirds often ceased foraging during heavy afternoon rains. Hard afternoon rains usually lasted ≤ 1 h, however; failure to account for the remaining daylight hours, during which hummingbirds foraged, in some standard fashion would create a much more serious underestimate.) Throughout each observation period, I sat or stood quietly 10–30 m from the plant(s) observed; my presence rarely if ever affected hummingbird activity. If observing a large shrub or tree, I visually apportioned flowers into four areas: top outside, top inside, lower outside, and lower inside flowers. Outside flowers were those extending beyond the foliage or exposed in the outer layer of foliage. At the end of each observation period, I counted the number of flowers in each area and the total number of flowers in the plant(s) observed.

During the observation period, I noted all visible or audible hummingbird activity related or unrelated to the observed flowers, including fly-catching or foliage-gleaning for insects. Each bird was identified to species, individual, and sex if possible. These data provided an independent census of species populations and aggressive interactions. I recorded these and other observations on a tape recorder.

I watched each hummingbird that visited observed flowers through 6 × 30 binoculars, noting species, sex, mark if any, and general feeding behavior, including vocalizations and visual displays. I counted the total number of flowers the bird visited, including repeats. In trees or shrubs, I kept track of the number visited in each of the four areas. With a stopwatch I recorded the cumulative time spent probing flower corollas, disregarding time the bird spent flying between flowers. Finally, I noted whether the visit ended voluntarily or involuntarily (interference from another bird), whether the bird perched after feeding, and in which direction it flew. During the 14 mo I counted a total of 81,996 flowers visited.

The nectar and arthropod contents of individual flowers were also investigated. I looked for arthropods in the corollas of a 10- to 50-flower sample of each hummingbird-exploited species. In five humming-

bird-pollinated species (*Inga brenesii*, *Malvaviscus arboreus*, *Hamelia patens*, *Lobelia laxiflora*, and *Cuphea* sp.), I also determined the effects of time of day and of visit frequency on nectar production. The evening before making the measurement, I used capillary tubes to remove all nectar from a sample of 45–120 flowers on one plant (*Inga*, *Hamelia*) or on plants growing in close proximity (*Malvaviscus*, *Lobelia*, *Cuphea*). A paper sack was then fastened over each inflorescence. At dawn, I measured overnight nectar production in all flowers with 10- or 25- $\mu$ l measuring capillaries. I measured one subsample of flowers every hour thereafter, a second subsample every second hour, and a third subsample only at dusk, keeping all flowers bagged between measurements to prevent nectar removal by visitors. Whenever time and flower numbers permitted (hourly in *Inga*, *Hamelia*, *Cuphea* but only twice each in *Malvaviscus* and *Lobelia*), I also measured extant nectar in unbagged flowers some distance from the bagged plants.

To measure changes in the numbers of arthropods available to foliage-gleaning hummingbirds, every other month I took one 200-sweep sample each in the scrub of Plot C and Plot I, and one in the mature forest understory of Plot H. Each sample was taken at chest height along a consistent route and under similar weather conditions. I sorted each sample to arthropods presumed edible by hummingbirds (smaller spiders, dipterans, hymenopterans, coleopterans, aphids, and lepidopteran larvae) or presumed inedible (orthopterans, most heteropterans, and larger individuals of other groups). Samples were preserved in 70% ethanol.

#### THE RESOURCE BASE

##### *Foliage arthropods*

Sweep sample data suggest that foliage arthropods were most numerous in Plot I during the early dry season and most numerous in Plot C during the wet season (Fig. 3). Arthropod biomass varied out of phase with numbers, however, and neither abundance nor biomass fluctuated greatly in either plot.

##### *Flowers*

Flowers of 15 plant species—all, with the possible exception of *Acnistus arborescens*, native to the area—and fruits of one species provided the hummingbirds in the study habitats with a constantly changing spectrum of food sources. Table 1 gives the distribution of these species among plots. Flowering (fruiting) peaks of the four successional trees, four shrubs, four forbs, three vines, and one epiphyte diverged greatly in phenology and intensity (Table 1). One shrub, one tree, and one forb produced flowers especially popular with hummingbirds, which apparently served as their principal pollen vectors.

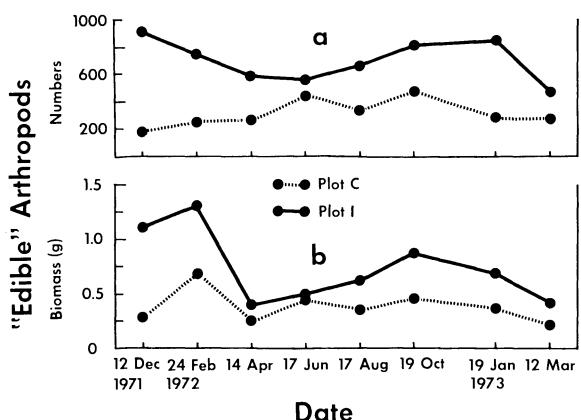


FIG. 3. Foliage arthropod abundance. (a) Numbers and (b) biomass of arthropods presumed edible by hummingbirds (see text) taken in 200-sweep samples.

Dense flower aggregations of these species were consistently defended by territorial hummingbirds (see below), and were operationally defined as "high flower densities."

*Hamelia patens* (Rubiaceae).—Larger shrubs of this species had some tubular orange-red flowers year-around (Fig. 4a) and produced high flower densities ( $\geq 70$  flowers per bush) May–October. The total number of *Hamelia* flowers available on all study plots never exceeded 500. Nevertheless, these popular flowers sustained hummingbird populations over a time of the year when other food sources were few. The relatively large volume of nectar produced (Table 1) explained both the popularity of *Hamelia* flowers and the low number necessary to support a territorial bird. Measured in the wet season, nectar production was greatest in midmorning (Fig. 5a); unbaged flowers investigated late in the day often lacked measurable amounts. During the dry season, some flowers lasted through midday only, then withered and fell off the shrub.

*Inga brenesii* (Leguminosae).—Common on most plots (Table 1), this successional evergreen tree also provided flowers year-around (Fig. 4b). From June through December, some larger individuals had high flower densities (600–6,000 flowers per tree). I observed a flowering peak in October–November 1971 similar to that in 1972. The yellow-white, *Mimosa*-like flowers exhibited few symptoms of the "ornithophily syndrome" (Faegri and van der Pijl 1971) and appeared unlikely candidates for hummingbird food sources. Nevertheless, the species may be in the process of adapting to bird pollination (P. Feinsinger, personal observation). Despite the small amount of nectar produced, hummingbirds visited the flowers frequently, especially in trees with fewer flowers (Table 1). First- and second-day flowers produced most nectar early in the morning (Fig. 5b);

TABLE 1. Characteristics of plant species exploited by hummingbirds in the successional transition-zone habitats.  
 T = tree; S = shrub; s = subshrub; F = forb; V = vine; E = epiphyte

Plant species	Plots	Flowers produced	Peaks <sup>a</sup>	Max number of flowers <sup>b</sup>	Length of enclosed corolla (mm)	Corolla insects <sup>c</sup>	Nectar/flower·24 h <sup>d</sup> (μl)	Visits/flower·day <sup>e</sup>
<i>Hamelia patens</i> (S)	I,J	All year	May–Oct	475 (Jun '72)	15–20	x	12.4	9.34; 10.18 high, 6.48 low
<i>Inga brenesii</i> (T)	B,C,E, G,J,K	All year	Sep–Nov	40,074 (Oct '72)	16–23	XX	0.8	1.68; 1.24 high, 5.09 low
<i>Lobelia laxiflora</i> (F)	I,J,K, O	Sep–Jun	Feb–May	55,941 (Apr '72)	17–21	x	16.2	0.99; 0.86 high, 4.22 low
<i>Malvaviscus arboreus</i> (S)	C,I,J, K	All year	Dec–Mar	94 (Feb '73)	27–35	x	8.9	3.36
<i>Cuphea</i> sp. (s)	I,J	Jun–Jan	Jun–Dec	430 (Jul '72)	21–26	x	1.8	1.17
<i>Justicia</i> sp. (s)	C,G,I	Feb–May	Mar–Apr	320 (Apr '72)	15–18	0		0.23
<i>Kohleria spicata</i> (F)	C,K	Sep–Feb	Oct–Jan	39 (Nov '72)	11–16	0		1.71
<i>Psittachanthus lateriflorus</i> (E)	J	Aug–Oct, Jan–Apr	Sep–Oct, Feb–Apr	36 (Mar '73)	12–17	0		10.81
<i>Mandevilla veraguensis</i> (V)	I,G	May–Aug	May–Aug	6 (Jun '72)	?	?		2.33
<i>Manettia flexilis</i> (V)	I	Dec–Feb	Dec–Feb	8 (Jan '73)	11–13	0		1.50
<i>Inga</i> sp. 2 (T)	G,J,K, O	Oct–Feb	Nov–Dec	7,420 (Nov '72)	7–8	XX		0.12
<i>Aenistus arborescens</i> (T)	C,I,J	Jan–Apr, Jun–Jul	Feb–Mar	4,818 (Mar '72)	5–8	x		0.10
<i>Lantana hispida</i> (F)	C,I,K	Aug–Jan	Aug–Oct	794 (Sep '72)	4–5	0		0.39
<i>Cirsium costaricense</i> (F)	C,I,J	Irregular	Apr–May	52 (May '72)	—	XX		0.54
<i>Ipomoea cathartica</i> (V)	I,J,K	Sep–Jan	Oct–Nov	744 (Nov '72)	40–44	XX		1.91
<i>Cecropia obtusifolia</i> <sup>f</sup> (T)	C,G,I, J,K	Apr–Jun	Apr–Jun	765 (May '72)	—	x		1.86

<sup>a</sup> Months in which number of flowers is 25% or more of the maximum.

<sup>b</sup> Maximum of the 14 2-mo rolling averages of flowers counted on all study-habitat plots.

<sup>c</sup> XX = > 0.5 arthropod/flower; x = < 0.5 arthropod/flower.

<sup>d</sup> Mean of all flowers measured (ages and measuring schedules pooled).

<sup>e</sup> Mean of all observation data over 14 mo. High = observations at high flower densities; low = observations at low flower densities.

<sup>f</sup> Fruits.

new flowers opened in late morning. Nectar was available throughout the day. Many small insects inhabited the corollas (Table 1) and may have provided additional food for hummingbirds. This species will be termed simply *Inga*, as opposed to *Inga* sp. 2.

*Lobelia laxiflora* (*Campanulaceae*).—This forb produced bright orange-red flowers for 10 mo of the year (Fig. 4c). High flower densities, comprising at least 300 flowers per 20 × 20-m plot segment, existed from February through May. Densities in Plot O sometimes reached 12,000 flowers per segment. These aggregations consisted of many juxtaposed individual plants, each with a few flowers only; as such, they differed from *Inga* or *Hamelia* high flower densities, which consisted of many flowers on single, discrete individuals. Flowers produced most nectar in early morning but continued to produce moderate amounts through the day and even increased production toward evening (Fig. 5c). In low densities, at least, flowers were quite popular (Table 1).

Five other plant species evidently adapted for bird pollination never produced high flower densities. Nevertheless, their flowers (and other flowers dis-

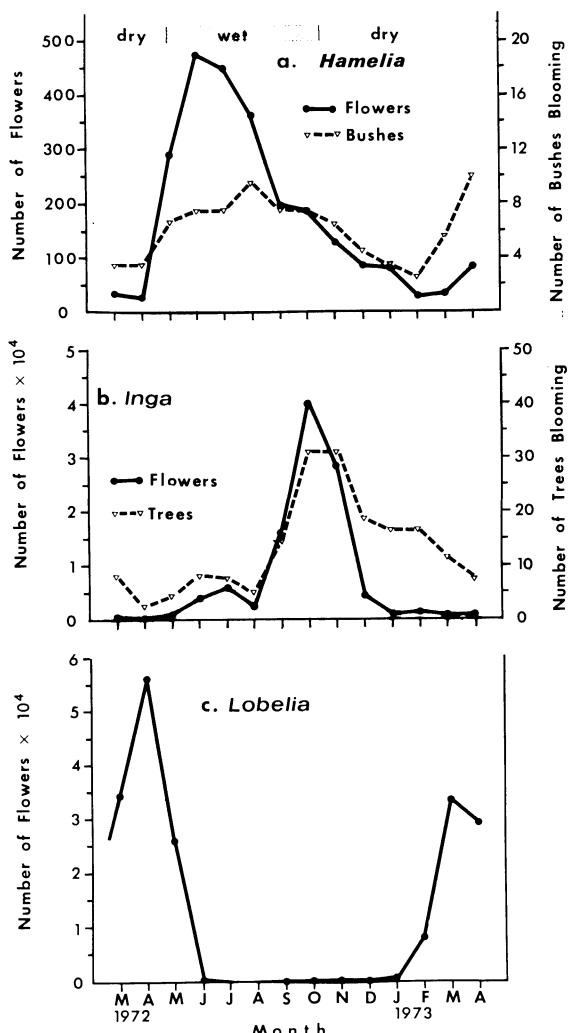


FIG. 4. Flowering phenology of the three most important species. Two-month rolling averages of total flowers counted (and trees or shrubs in flower) on study habitat plots at each month's end, for (a) *Hamelia patens*; (b) *Inga brenesii*; (c) *Lobelia laxiflora*.

cussed later) enriched the resource base and provided food for many hummingbirds.

*Malvaviscus arboreus* (*Malvaceae*).—Some individuals of this forest understory shrub grew in Plot I and other open sites. Their long, red flowers produced relatively large amounts of nectar early in the day (Table 1; Fig. 5d) and attracted hummingbirds throughout the year. Longer-billed species probed flowers from the front. Smaller, shorter-billed hummingbirds often probed between the petals.

*Cuphea sp.* (*Lythraceae*).—This low “subshrub” (*sensu* Whittaker 1970) put out orange, tubular flowers from June through January (Table 1). Flowers produced small amounts of nectar throughout the day (Fig. 5e) and attracted one hummingbird species (*Chlorostilbon canivetii*).

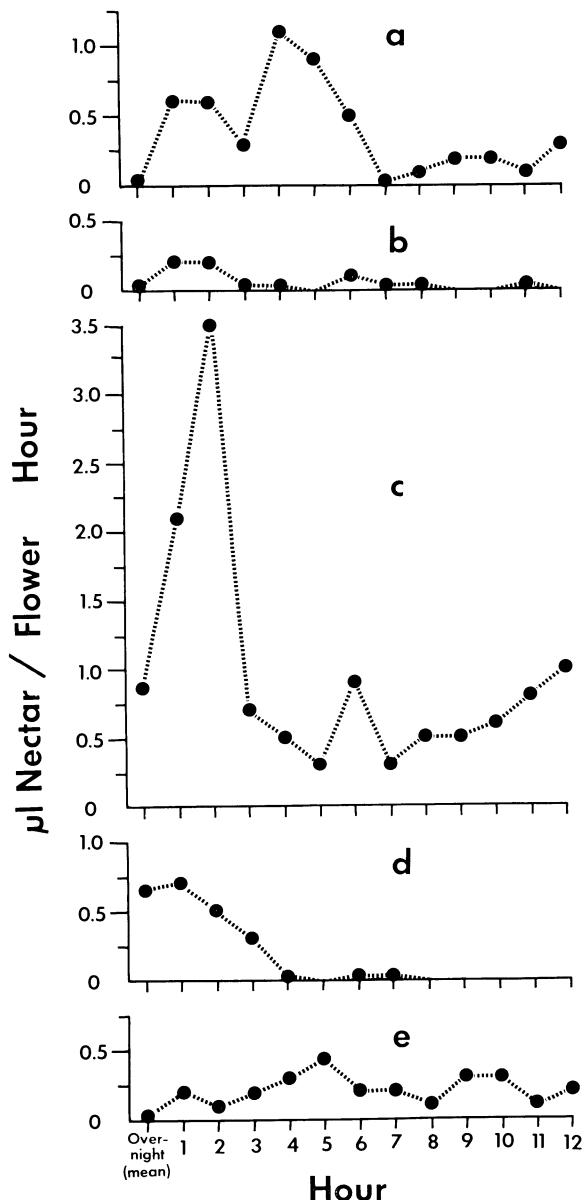


FIG. 5. Nectar production. Mean volume of nectar produced per flower, beginning at daybreak. Overnight production is mean of 12 hours' accumulation. Data from flowers checked at intervals longer than 1 h (see text) not included. (a) *Hamelia patens*; (b) *Inga brenesii*; (c) *Lobelia laxiflora*; (d) *Malvaviscus arboreus*; (e) *Cuphea* sp.

*Justicia sp.* (*Acanthaceae*).—This subshrub produced pink flowers, which received sporadic hummingbird visits, from February through May.

*Kohleria spicata* (*Gesneriaceae*).—The bright orange-red flowers of this forb stood out on open hillsides from September through February and attracted several hummingbird species.

*Psittacanthus lateriflorus* (*Loranthaceae*).—This

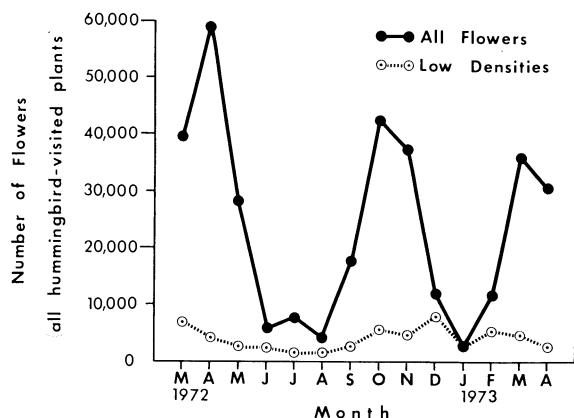


FIG. 6. Total flower numbers. Flowers of all hummingbird-exploited plant species (plus *Cecropia obtusifolia* fruits) included. Two-month rolling averages of all such flowers (solid line) and all such flowers not in high densities (dashed line) counted on study habitat plots at each month's end.

epiphyte exhibited a bimodal flowering pattern. Although uncommon, its bright orange flowers received consistent attention from hummingbirds (Table 1).

*Mandevilla veraguasensis* (Apocynaceae) and *Manettia flexilis* (Rubiaceae), two uncommon vines on Plot I, may or may not have been adapted for hummingbird pollination but received hummingbird visits nonetheless. Hummingbirds also visited six plant species apparently adapted for other pollinators entirely. These included two tree species with whitish flowers (*Inga* sp. 2, Leguminosae, and *Acnistus arborescens*, Solanaceae), and the white-flowered forb *Lantana hispida* (Verbenaceae), the thistle *Cirsium costaricense* (Compositae), and the vine *Ipomoea cathartica* (Convolvulaceae). (The birds preferred *Ipomoea* flowers part or all of whose corollas had been eaten by squirrels and whose nectaries were therefore more easily accessible.) Finally, hummingbirds fed on liquid exuded from partly eaten fruits of the common successional tree *Cecropia obtusifolia* (Moraceae) that were left hanging by frugivorous birds and mammals. Each fruit thus resembled a nectar-producing flower, and will be classed as a flower below.

Total numbers of hummingbird food sources (flowers and *Cecropia* fruits) fluctuated widely (Fig. 6), the peaks reflecting heavy flowering by *Inga* and *Lobelia*. Since flowering bursts of these and other species tended to recur annually (Fig. 4; Table 1), total flower numbers also displayed an annually periodic pattern. Janzen (1967a) and Wolf (1970) predicted that overall flower production on the Pacific slope of Central America should peak in the dry season. Of the three most popular plant species in the study habitats, however, one (*Hamelia*) peaked

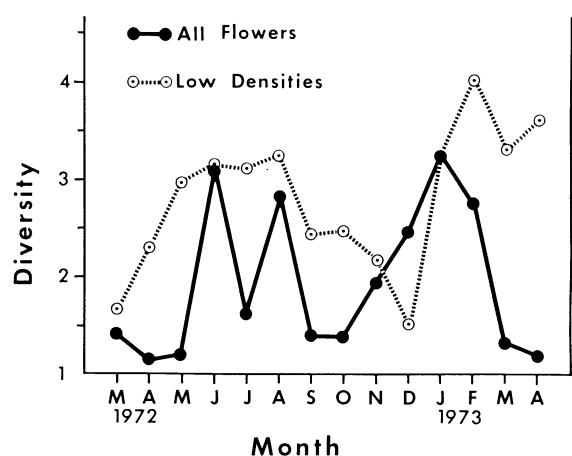


FIG. 7. Flower diversity. Flowers counted as in Fig. 6; solid line is diversity of all flowers ( $D_{Fm}$ ; Eq. 1), dashed line is diversity of flowers not in high densities.

through the wet season, one (*Inga*) through late wet and early dry seasons, and one (*Lobelia*) in the late dry season (Fig. 4). Considering flowers of each species or high and low flower densities of the three major species as separate biotic "resource states" (*sensu* Colwell and Futuyma 1971), at no time of year were fewer than eight or more than thirteen biotic resource states available. Numbers of flowers not located in high densities fluctuated far less than total flower numbers, and remained at a consistent level throughout the year (Fig. 6).

Flower diversity in a given month ( $m$ ) is

$$D_{Fm} = 1 / \sum_{r=1}^{R_m} p_{rm}^2, \quad (1)$$

where  $p_{rm}$  is the ratio of flowers available in biotic resource state  $r$  to flowers available in all  $R_m$  resource states.  $D_{Fm}$  measures the inverse of "dominance concentration" and is affected less by the number of classes counted than by the dispersion of observations among classes (Hill 1973). Changes in flower diversity were thus nearly opposite to changes in flower abundance (Fig. 7), since large numbers of flowers signified a flowering burst of a single plant species (Fig. 6). Correlation between flower abundance and diversity was highly negative ( $r = -0.7682$ ,  $p < .01$ ). Nevertheless,  $D_{Fm}$  also reflected changes in richness, or the number of biotic resource states ( $R_m$ ), over the 14 mo ( $r_s = .6148$ ,  $p < .02$ ).

Diversity of low-density flowers varied less regularly (Fig. 7) because of variation in the *Inga*, *Hamelia*, and *Lobelia* entering the class of high flower densities. The low value for March 1972 corresponded to a preponderance of low-density *Lobelia* flowers, the low of December 1972 to a peak in *Inga* sp. 2 and a scarcity of other flowers.

## THE GUILD

*Territorial and traplining strategies*

Some hummingbirds specialize on resource clumps that produce large quantities of nectar. To ensure exclusive use of this nectar, these birds set up feeding territories (Pitelka 1942; Wolf 1969, 1970). A single rich clump may provide enough nectar to satisfy a bird's entire daily energy requirements, or a large part thereof, and is defended as a "static territory." Several less rich clumps may be exploited and defended in succession as a "shifting territory" (not *sensu* Wolf 1970). The territory holder, or resident, should be conspicuous and aggressive, excluding not only conspecifics but also individuals of other species if the energetic expense of such aggression is less than the potential energy loss to birds not excluded (Orians and Willson 1964). Competitive interference may result (see Brian 1956, Miller 1967, Case and Gilpin 1974). It follows that territorial behavior is adaptive only when nectar dispersion, quantity, and quality ensure that energy expended in feeding and defense can be balanced by the energy obtained from the territory (Stiles and Wolf 1970, Linhart 1973, Stiles 1973). For a territorial bird, the resource gradient is coarse-grained (MacArthur and Levins 1964, MacArthur 1968), and the territorial bird should neglect dispersed, low-yield flowers.

In contrast, birds excluded from rich resource clumps by territorial individuals, or faced with a resource spectrum lacking rich clumps, should employ a generalist strategy that makes use of the dispersed, low-yield resources (Ashmole 1968, MacArthur 1972, Cody 1974). Subordinate hummingbirds sometimes exhibit "traplining" behavior (Colwell 1973, Linhart 1973, Feinsinger and Chaplin 1975; see Janzen 1971), following a regular feeding route between successive low densities of flowers on scattered trees, shrubs, vines, and herbs. Unlike a territorial bird, which may perch for considerable lengths of time between feeding and fighting bouts (see Pitelka 1942, Stiles and Wolf 1970, Lyon 1973), a subordinate trapliner spends considerable time in flight, seldom if ever defending an individual flower clump. To a trapliner, the resource spectrum provides a fine-grained mixture; to maximize energy intake, this bird should neglect few resources encountered. Evidence suggests that those trapliners without specialized bills possess morphological adaptations that allow slow, searching flight and conserve energy, but lack the adaptations for aggressive behavior characteristic of territorial birds (Feinsinger and Chaplin 1975). Competition among such nonaggressive species may involve exploitation rather than interference but may also result in competitive displacement if

efficiencies differ (see Jaeger 1974, Colwell and Fuentes 1975).

The contrast between traplining and territorial behavior is rarely absolute. Birds may exploit dispersed flowers without following regular traplines. Some species employ both strategies. Among North American hummingbirds, at least, territories may be complicated by mating functions (see Pitelka 1942, 1951; Legg and Pitelka 1956; Stiles 1973). Nevertheless, in many simpler tropical communities studies of the nectarivorous bird guild reveal a dichotomy of species or sexes that defend the rich, compact flower clumps and others that exploit the less attractive, undefended flowers (e.g., Wolf 1970, Colwell 1973, Linhart 1973, Wolf et al. 1976). The Monteverde hummingbirds, in particular the two species most continuously present, displayed such a dichotomy.

*The principals*

*Amazilia saucerottei* (hereafter termed *Amazilia*, as distinct from *A. tzacatl*), Blue-vented Hummingbird, is a medium-sized territorial species that dominated most rich food sources throughout the study period and greatly affected the foraging patterns of all other species. All individuals observed (except recently fledged immatures) possessed similar plumage and exhibited similar behavior; measurements of netted birds revealed no obvious bimodal patterns (Table 2). Since both sexes are known to be aggressive (Stiles and Wolf 1970), I assumed that the territorial birds I observed included both males and females. Many individuals, particularly immatures, were transients; out of 126 birds I marked, only 3 remained in the study area consistently. All interchange evidently occurred with populations at lower elevations; I observed few *Amazilia* in mature forest or in higher, more mesic openings. Wolf (1970) recorded population highs of this species in lowland Guanacaste in January and June 1967, two of the three months of 1972–1973 during which flower numbers in the study habitats were lowest (cf. Fig. 6).

Resident *Amazilia* advertised by flicking their steel-blue tails and performing a wide vocal repertoire (Table 2). Nevertheless, other hummingbirds often entered defended clumps. Residents chased or attempted to chase intruders for some distance, often leaving territories undefended for a short time; other birds often foraged among these undefended flowers. Most observed aggressive encounters were intra-specific (Table 3), simply reflecting the concentrations of this species at high flower densities. *Amazilia* was dominant over most other species. Only *Amazilia tzacatl*, which also dominates *A. saucerottei* in lowland Guanacaste (Wolf 1970), and *Lampornis calolaema* consistently won encounters with this species.

TABLE 2. Characteristics of hummingbird species constituting the nectarivorous bird guild in the study habitats. Means and sample sizes given for weights and measurements; where not separated, sexes indistinguishable in the hand

Species	Sex	Body wt (g)	Wing length (mm)	Culmen from base (mm)	Flower foraging strategy <sup>a</sup>	When present	Insect foraging <sup>b</sup>	Vocalizations (n)
<b>1. Core species</b>								
<i>Amazilia saucerrottei</i> ( <i>As</i> )	♂, ♀	4.45 (126)	53.9 (119)	23.2 (119)	T	All year	fc	7
<i>Chlorostilbon canivetii</i> ( <i>Cc</i> )	♂	2.62 (7)	46.2 (6)	17.5 (6)	t	Jan–Nov	fg	2
<i>Philodice bryantae</i> ( <i>Pb</i> )	♀	3.31 (5)	41.4 (5)	19.6 (5)	T	Sep–Apr	fc	4
<i>Colibri thalassinus</i> ( <i>Ct</i> )	♂, ♀	3.42 (5)	42.0 (2)	20.2 (2)	ft	Oct–Apr, Jun	fg	3
<b>2. Species with populations centered at lower elevations</b>								
<i>Hylocharis eliciae</i> ( <i>He</i> )	♂, ♀	3.59 (6)	47.7 (5)	20.9 (5)	T (ft?)	Oct–Nov, Feb–Apr		
<i>Archilochus colubris</i> ( <i>Ac</i> )	♂	2.80 (4)	36.7 (3)	21.1 (4)	T? ft?	Nov–Mar		
<i>Heliodoxa constantii</i> ( <i>Hc</i> )	♀	2.93 (2)	42.2 (2)	21.0 (2)	t?	May–Aug		
<b>3. Species with populations centered in forested habitats</b>								
<i>Eupherusa eximia</i> ( <i>Ee</i> )	♂	4.48 (50)	59.4 (48)	23.0 (43)	ft	All year		
<i>Campylopterus hemileucurus</i> ( <i>Ch</i> )	♀	3.97 (31)	54.6 (30)	22.8 (29)	t?			
<b>4. Species with populations centered in higher, more mesic habitats</b>								
<i>Lamprolais calolaema</i> ( <i>Lc</i> )	♂	5.60 (7)	60.6 (7)	23.2 (7)	T ft?			
<i>Elvira cupreiceps</i> ( <i>Ec</i> )	♀	4.23 (2)	55.5 (2)	23.0 (2)	ft?			
<i>Phaethornis longuemareus</i> ( <i>Pl</i> )	♂, ♀	3.22 (3)	47.8 (3)	18.2 (3)	?	May '72		
<i>Colibri delphinae</i> ( <i>Cd</i> )	♂, ♀	3.02 (3)	45.5 (2)	19.0 (2)	ft?	Oct '72		
<i>Amazilia tzacatl</i> ( <i>At</i> )	♂, ♀	5.12 (5)	57.2 (5)	25.7 (5)	T	Sporadic; Jun, Apr		

<sup>a</sup> T = territorial; t = trapliner; ft = facultative trapliner.<sup>b</sup> fc = aerial fly-catching from perch; fg = foliage-gleaning.

*Chlorostilbon canivetii*, Fork-tailed Emerald, was the smallest bird commonly observed (Table 2) and the most consistent and apparently most efficient of any species at exploiting dispersed flowers. These birds occurred in the study habitats throughout this study except in December 1971–early January 1972 and December 1972–early January 1973. Just before and after each hiatus, I saw *Chlorostilbon* solely in lower study areas, which suggested that the population migrated to lower elevations. Diversity of low-density flowers was lowest at this time; hummingbird-visited flowers in certain lowland Guanacaste habitats are most diverse during December and early January (P. A. Opler, *personal communication*),

however, and *Chlorostilbon* exploits many of the less dense clumps of these (Heithaus 1974, P. A. Opler, *personal communication*). I never observed individuals in the forest or at higher elevations. Two marked birds in particular, a male and a female, consistently traplined flowers in Plot I. I followed the female along much of her route for most of one day, and often observed other traplining birds of both sexes for several minutes at least. Each bird flew slowly from flower clump to clump near ground level, investigating the surrounding vegetation and occasionally gleaning foliage insects. Clumps were revisited in nearly the same sequence; the interval between successive visits usually lengthened through

TABLE 3. Aggressive encounters. All interspecific encounters with a clear winner included; all intraspecific encounters included regardless of outcome. For abbreviations of species names, see Table 2

Loser	Winner													Total encounters	Inter-specific wins (%)		
	<i>As</i>	<i>Cc</i>	<i>Pb</i>	<i>Ct</i>	<i>He</i>	<i>Ac</i>	<i>Hc</i>	<i>Ee</i>	<i>Ch</i>	<i>Lc</i>	<i>Ec</i>	<i>Pl</i>	<i>Cd</i>	<i>At</i>			
<i>As</i>	1	1	11 <sup>a</sup>	3 <sup>d</sup>	0	0	6	1	15	0	0	0	0	7	296	1,361	84.8
<i>Cc</i>	68 <sup>a</sup>	0 <sup>b</sup>	2 <sup>d</sup>	4 <sup>ad</sup>	0	1	1	0	0	0	0	0	1	84	24 <sup>b</sup>	8.3	
<i>Pb</i>	82	6 <sup>c</sup>	6 <sup>a</sup>	12 <sup>a</sup>	0	0	3	0	9	0	0	1	0	121	96	1.7	
<i>Ct</i>	27 <sup>a</sup>	0	0	0	0	0	1 <sup>d</sup>	0	0	0	0	0	0	60	21	53.3	
<i>He</i>	33 <sup>a</sup>	0	1	3	0	0	1	0	0	0	0	0	0	63	4	38.7	
<i>Ac</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Hc</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	100	
<i>Ee</i>	28	0	0	7 <sup>a</sup>	6 <sup>a</sup>	0	0	0	5	0	0	0	1	66	25	28.8	
<i>Ch</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	2	4	50.0	
<i>Lc</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	29	0	100	
<i>Ec</i>	8 <sup>a</sup>	0	0	2	0	0	0	7	0	0	0	0	0	17	14	0	
<i>Pl</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cd</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	100	
<i>At</i>	4	0	0	0	0	0	0	0	0	0	0	0	0	13	0	69.2	

<sup>a</sup> All interactions but one at high-density *Lobelia laxiflora*.

<sup>b</sup> All interactions but four at high-density *Lobelia laxiflora*.

<sup>c</sup> All interactions at high-density *Lobelia laxiflora*.

<sup>d</sup> Many attempted displacements of row species by column species failed.

the day as nectar production, especially in *Hamelia* flowers, declined. This method of exploiting dispersed nectar sources apparently inhibited foraging by other nonterritorial species, which visited dispersed flowers consistently only when *Chlorostilbon* populations were low, and may also have prevented the intrusion of other *Chlorostilbon*. I noted few instances in which these traplines overlapped and saw only four encounters between trapliners.

*Chlorostilbon* exploited undefended clumps and even isolated flowers of every plant species described above except *Mandevilla*. These birds did not avoid richer clumps by choice, however. Individuals often visited high-density *Hamelia*, occasionally high-density *Inga*, but these flowers were usually defended by an *Amazilia*, which immediately chased the intruder. In contrast, the *Amazilia* and other aggressive birds that assembled at *Lobelia* fields constantly disputed their indefinite territorial boundaries with each other and usually ignored inconspicuous trespassers such as *Chlorostilbon*. When attacked by a resident, a *Chlorostilbon* just moved a short distance and continued to feed, or dove lower into the vegetation. Many *Chlorostilbon*, especially immatures, converged on these *Lobelia* fields. This unusual situation led to many intraspecific and interspecific encounters (Table 3).

#### Other core species

Through much of this study two additional populations centered in the successional transition-zone habitats, and relied on the flowers sampled by the census scheme no less than did the *Amazilia* and *Chlorostilbon* populations. These four species thus constituted the core of the guild.

*Philodice bryantae*, Magenta-throated Wood-star. Both sexes of this species superimposed intraspecific feeding territories over high-density *Lobelia* and both densities of *Inga* simultaneously defended by *Amazilia* or other territorial birds. *Philodice* apparently presented few sign stimuli that might elicit attack from other species. When discovered, these birds were invariably displaced (Table 3), but more often they foraged in these rich flower clumps unmolested by the dominant residents. Small and compact (cf. Table 2), individuals were often mistaken for bees by local Costa Ricans and visiting birders. Both sexes resembled hymenopterans not only in general configuration and dull coloration—male gorgets apparently reflected light only when deliberately displayed—but also in tone of wingbeat and in slow, deliberate manner of feeding. Furthermore, *Philodice* concentrated on *Inga* flowers in those upper areas preferred by large *Pepsis* (Hymenoptera: Pompilidae) and *Eulaema* or *Bombus* (Apidae), regions perhaps difficult for *Amazilia* to survey from their perches on lower, inner branches. *Philodice* individuals attacked conspecific intruders vigorously, watching over their flowers from perches nearby; males sang from these perches and performed aerial displays. These birds were abundant when *Inga* and *Lobelia* flowers were abundant—from September through March (1973) or April (1972)—but I could not discover where they spent the remainder of the year. The population was most dense in the study habitats; a few individuals occurred in higher openings, but I observed none in the forest.

*Colibri thalassinus* (hereafter termed *Colibri*, as distinct from *C. delphinae*), Green Violet-ear. *Colibri* is morphologically specialized for neither territorial

nor traplining behavior (Feinsinger and Chaplin 1975). A highly migratory bird (Wagner 1945, Slud 1964, Skutch 1967, Wolf 1969), in high-altitude communities this species often capitalizes upon seasonal resource flushes and sets up feeding territories (Colwell 1973, Colwell et al. 1974), but may be ejected by more efficient birds when food becomes scarce (Wolf et al. 1976). At Monteverde, when *Inga* and *Lobelia* were especially abundant, *Colibri* visited high flower densities and frequently ignored attacks from resident *Amazilia* or other territorial birds. *Colibri* lost several of these encounters, however (Table 3), and never maintained definite feeding territories. Instead, individuals moved from clump to clump and rarely attempted to displace other birds (except at especially dense *Lobelia*). Three birds netted at *Lobelia* patches in March and April 1972 foraged in the same areas a year later. In the dry-season months between *Inga* and *Lobelia* flowering bursts, when *Chlorostilbon* populations were low, *Colibri* avoided high flower densities and exploited low-density flowers through foraging patterns that approached true traplines. Thus *Colibri* acted as a facultative trapliner. Males sang from perches some distance from feeding sites and may have defended breeding territories. The population was most dense in the study habitats, but some birds resided in higher clearings. I observed no *Colibri* between mid-June and early October 1972; these birds may go to lower (Skutch 1967) or higher elevations.

#### *Peripheral species*

Populations of three species that visited flowers in the study habitats apparently centered in successional habitats at lower elevations (Slud 1964).

*Hylocharis eliciae*, Blue-throated Goldentail. Many *Hylocharis* immatures and some adults visited *Lobelia* February–April 1972 and again February–April 1973; a few individuals visited *Inga* in October and November 1972. These birds set up feeding territories and attacked intruding *Amazilia* or other birds, but often lost encounters with the larger *Amazilia* (Table 3).

*Archilochus colubris*, Ruby-throated Hummingbird. Similar in general appearance to *Chlorostilbon* females, females of this North American migrant exploited flowers in the study habitats January–March 1972 and November 1972–March 1973. These birds occasionally visited high-density *Inga*, and when *Chlorostilbon* populations were low *Archilochus* exploited a variety of undefended flowers. Males, which defend feeding and breeding territories during the summer (Bent 1940, Pitelka 1942), were sometimes netted (Table 2) but were observed feeding solely at high-density *Lobelia* in February and March 1972.

*Heliomaster constantii*, Plain-capped Starthroat. In the dry lowlands, this species visits a variety of

flowers (Wolf 1970, Heithaus 1974, P. Opler, personal communication). In the study habitats, however, *Heliomaster* visited only the vine *Mandevilla*, from May through August 1972.

Two conspicuous species most regularly exploited flowers in the forest of the transition zone and higher regions:

1) *Eupherusa eximia*, Stripe-tailed Hummingbird. *Eupherusa* was perhaps the most abundant hummingbird of the Monteverde region. Males, at least, were very aggressive and often territorial in forested habitats. In the study habitats, both sexes usually lost encounters with *Amazilia* (Table 3), and often exploited scattered *Malvaviscus*, *Psittacanthus*, *Lobelia*, *Kohleria*, and *Manettia* flowers. Whenever *Amazilia* was absent from a richer resource clump, such as high-density *Inga* or *Hamelia*, either a male or female *Eupherusa* invariably set up a territory.

2) *Campylopterus hemileucurus*, Violet Sabrewing. The largest hummingbird encountered (Table 2), *Campylopterus* often flew into mist nets and occasionally visited observed *Inga* or *Malvaviscus* flowers.

Two species most commonly remained in higher, more mesic communities:

1) *Lampornis calolaema*, Purple-throated Mountain-gem. *Lampornis* sometimes set up territories at high-density *Inga*. Larger than the core species and *Eupherusa* (Table 2), conspicuous, and aggressive, these birds lost no observed encounter (Table 3).

2) *Elvira cupreiceps*, Coppery-headed Emerald. These vocal, conspicuous little birds, which occasionally visited observed *Psittacanthus* or *Inga*, never won an observed interspecific encounter (Table 3).

I could not discover the central populations from which the observed individuals of three species derived:

1) *Phaethornis longuemareus*, Little Hermit. I observed two *Phaethornis* visits to a *Malvaviscus* in May 1972.

2) *Colibri delphinae*, Brown-Violet-ear. At least two *C. delphinae* visited high-density *Inga* in October 1972. This large, short-billed species (Table 2) may be even more highly migratory and less specialized than *C. thalassinus* (Slud 1964).

3) *Amazilia tzacatl*, Rufous-tailed Hummingbird. Several *A. tzacatl* defended high-density *Hamelia* in June 1972, and one individual briefly visited high-density *Lobelia* in April 1973. Slightly larger than *A. saucerottei* (Table 2), *A. tzacatl* often won encounters (Table 3).

*Vermivora peregrina*, the Tennessee Warbler, visited *Malvaviscus* flowers in February 1972 and February 1973 but is not strictly a member of the nectarivore guild.

Additional data on distribution and behavior of the hummingbird species are presented elsewhere (Feinsinger 1976).

### RESOURCE PARTITIONING

The hummingbirds foraged in a variety of ways among a variety of food sources. The food selection patterns of some species interfered with the foraging of others. Such selection and exclusion resulted in the regular partitioning of food within several dimensions. All data on this resource partitioning are included in the analysis that follows this section.

#### *Partitioning in the plant dimension*

To attract hummingbirds, a flowering plant should possess a certain minimal set of characteristics, such as visually conspicuous, three-dimensional flowers (*Cecropia* is an exception), each containing reasonable quantities of food (Wolf 1970, Snow and Snow 1972). Beyond that, which hummingbird species exploit flowers of an individual plant or plant clump is determined by the habitat in which the plant grows, other species-specific characters of the plant, and the total food reward provided.

**Habitat.**—Habitat differences among hummingbird species lead them to exploit flowers on different individual plants and plant species (Wolf 1970, Linnhart 1973, Stiles 1975). The variety of habitat selection patterns among the 14 Monteverde species implies that nectar resources were partitioned along habitat dimensions. The *Eupherusa* populations, for example, exploited flowers on many plants not encountered by the core species. This study dealt with niche dimensions, however, which by definition involve a single community (Whittaker et al. 1973). The community was operationally defined by the hummingbirds' lack of discrimination among the various successional transition-zone habitats. Interspecific differences in habitat selection affected the integration of the guild as a whole but did not affect resource partitioning among guild members within the community considered.

**Other species-specific characters.**—Such characters as growth form, flower shape, and mean food reward per flower, which vary with species, influence flower selection in hummingbirds (see Wolf 1970, Snow and Snow 1972, Colwell 1973, Hainsworth 1973, Stiles 1975, Wolf et al. 1976). Thus partitioning of food resources involves plant species as proximate cues. Flowers of some species in the study habitats, such as *Cuphea*, produced small nectar rewards in dispersed flowers. Territorial birds in particular ignored these plants. In contrast, territorial birds exploited *Inga* despite the low food reward per individual flower, perhaps because they could rapidly visit several flowers in an inflorescence and often could perch while feeding. *Malvaviscus* plants provided flowers with large mean food rewards, and consistently attracted territorial species. Birds flying

in a certain manner consistently missed or ignored flowers on certain plants. *Colibri*, which usually foraged near the ground, often flew beneath *Inga* trees without stopping to feed. *Philodice* usually foraged in tall shrubs or trees, ignoring flowers of all species with less conspicuous growth forms except *Lobelia*. *Amazilia*, which characteristically flew swiftly and at tree level, snubbed flowers of such herb-layer species as *Justicia*, *Cuphea* and *Kohleria*. *Chlorostilbon*, which flew slowly through the scrub, seldom missed even single flowers on low-growing forbs.

**Resource density.**—Hummingbirds treated different individuals of 13 of the plant species more or less uniformly regardless of flower density. High flower densities of *Hamelia*, *Inga*, and *Lobelia* flowers, however, supported static territories that contrasted with the shifting territories or traplines incorporating low-density flowers of these and other species. Thus selection among conspecific plants on the basis of flower density resulted in further partitioning of food resources. Plant individuals or clumps of these three plants could be placed in "biotic resource states" by the flower density criterion as well as by species. For example, in July 1972 *Amazilia*, and *Eupherusa* and *Lampornis* as well, concentrated on plants with high flower densities, while *Chlorostilbon*, excluded from these, exploited scattered flowers of four plant species (Table 4).

#### *Partitioning in the spatial dimension*

Coexisting birds often forage in different spatial patterns, thereby partitioning their food resources (e.g., Betts 1955, MacArthur 1958, Hamilton 1962, Willson 1970). As shown above, divergent stratal preferences influenced the hummingbirds' selection of different plants. In addition, if several nectarivorous bird species select the same tree or shrub, food resources may be partitioned if different species concentrate on flowers in different regions (Colwell et al. 1974), such as the operational groupings (top outside, top inside, lower outside and lower inside) used in this study. "Spatial partitioning" then occurs when different bird species visiting an individual tree or shrub distribute flower-visits differently among these flower groups. These four "spatial resource states" are thus subdivisions of biotic resource states.

Spatial partitioning was often observed at high-density *Inga* trees, less often at low-density *Inga*, high-density *Hamelia*, and *Acnistus*. Since a resident bird attempted to exclude others from the entire plant, not just a portion, spatial foraging differences were seldom a direct result of aggression. Rather, a bird arriving at a shrub or tree already visited by other species would simply encounter more nectar per flower in areas that had received the least previous attention, and should therefore forage in a

TABLE 4. Example of partitioning in the plant dimension. Data for July 1972. First figure per cell: number of flowers visited during 7-h observation period. Figure in parentheses: utilization of biotic resource state by hummingbird population (see Eq. 2, Table 8, and text). Decimal:  $p_{irm}$ , or proportion of  $r$  in the diet of  $i$

Bird species ( $i$ )	Biotic resource state $r$							Effective population ( $U_{i..m}$ )	
	<i>Inga brenesii</i>		<i>Hamelia patens</i>		<i>Mandevilla veraguasensis</i>	<i>Cuphea</i> sp.	<i>Malvaviscus arboreus</i>		
	Low-density	High-density	Low-density	High-density					
<i>Amazilia</i>		534 (2297.8) .3703	5 (27.4) .0044	2986 (3877.1) .6247			2 (3.4) .0005	6205.7	
<i>Chlorostilbon</i>	14 (1146.0) .5254		21 (131.7) .0604	128 (166.2) .0762		47 (737.1) .3380		2181.0	
<i>Heliomaster</i>					5 (7.5) 1.0			7.5	
<i>Eupherusa</i>		278 (1196.2) 1.0						1196.2	
<i>Lampornis</i>		1078 (4638.6) 1.0						4638.6	
$U_{..rm}$	1146.0	8132.6	159.1	4043.3	7.5	737.1	3.4	14,229.0*	

\* Guild effective population, or  $U_{...m}$ .

spatial pattern different from other species' patterns (Colwell et al. 1974). Species-specific mannerisms produced consistent interspecific differences in these patterns. *Chlorostilbon* characteristically visited flowers in the lower regions of *Hamelia*; *Amazilia*, which often perched above shrub height, usually visited flowers in the upper branches. In contrast, *Amazilia* that defended *Inga* often perched on lower inside branches, visiting lower and inner flowers as frequently as flowers in other areas. *Philodice*, which perched high, usually visited flowers in upper and outer areas of those trees, perhaps also avoiding

potential harassment by the dominant residents. *Colibri* visited lower *Inga* flowers most consistently, while *Eupherusa*, normally inhabiting the forest understorey, often visited a greater number of lower inside *Inga* flowers than other bird species. Table 5 presents an example of spatial partitioning within a high-density *Inga* tree, in which not only were all interspecific differences in the spatial distribution of flower visits significant ( $X^2 = 1,735.2$ ,  $p < .001$ ), but all between-species comparisons were also significant ( $p < .01$ ) excepting the *Archilochus-Philodice* comparison.

TABLE 5. Example of partitioning in the spatial dimension. High-density *Inga brenesii*, 18 November 1972. Observed tree had 4,980 flowers (1,800 top outside, 740 top inside, 1,960 lower outside, 480 lower inside). Raw data; number of flowers visited in each area. Decimals: proportion of  $i$ 's visits made in spatial resource state  $k$  (see Eq. 12, Table 8)

Bird species ( $i$ )	Spatial resource state $k$							Total in tree	
	Top		Lower		outside	inside			
	outside	inside	outside	inside					
<i>Amazilia</i>	981 .3847	579 .2271	765 .3000	225 .0882				2,550	
<i>Philodice</i>	1,010 .8080	0	241 .1920	0				1,251	
<i>Colibri</i>	64 .1105	30 .0518	379 .6546	106 .1831				579	
<i>Archilochus</i>	370 .8277	8 .0179	59 .1320	10 .0224				447	
<i>Eupherusa</i>	0	0	37 1.0	0				37	
<i>Elvira</i>	18 .1084	42 .2530	94 .5663	12 .0723				166	

TABLE 6. Examples of partitioning in the diurnal dimension. Raw data; number of flowers visited in each hour of observation (number of feeding bouts/hour in parentheses). Decimals: proportion of *i*'s total visits made in hour (diurnal resource state) *h* (see Eq. 13, Table 8)

Bird species <i>i</i>	Hour (diurnal resource state) <i>h</i>							
	0500–0600	0600–0700	0700–0800	0800–0900	0900–1000	1000–1100	1100–1200	
<b>a. At high-density <i>Hamelia patens</i>, 5 Jun 1972</b>								
<i>Amazilia tzacatl</i>	383 (9) .7226	130 (3) .2453	17 (1) .0321					
<i>Chlorostilbon</i>	42 (1) .0384	226 (6) .2070	406 (5) .3718	160 (2) .1465	156 (3) .1429	55 (1) .0504	47 (2) .0430	
<i>A. saucerottei</i>	19 (1) .4130	12 (2) .2609	15 (2) .3261					
Hour (diurnal resource state) <i>h</i>								
	0515–0615	0615–0715	0715–0815	0815–0915	0915–1015	1015–1115	1115–1215	
<b>b. At high-density <i>Inga brenesii</i>, 24 Jul 1972</b>								
<i>Amazilia saucerottei</i>		14 (2) .0262	292 (5) .5468	186 (5) .3483	20 (1) .0375	13 (3) .0243	9 (3) .0169	
<i>Lampornis</i>	99 (1) .0918			172 (6) .1596	318 (12) .2950	208 (10) .1929	281 (14) .2607	
<i>Eupherusa</i>				266 (5) .9568	3 (1) .0108		9 (1) .0324	

### Partitioning in the diurnal dimension

Differences in foraging times that result in partitioning of renewing food resources occur among bees (Linsley et al. 1963, Schlising 1970), lizards (Pianka 1969, 1973), seabirds (Ashmole 1968), and shorebirds (Recher 1966). Similarly, if different hummingbird species visit the same flowers at different times, the renewing food resources in those flowers may be partitioned along a diurnal dimension. I shall define "diurnal partitioning" as interspecific differences in the diurnal distribution of flower visits within a single observed plant or clump, again treating "diurnal resource states" of nectar as subdivisions of biotic resource states.

As long as flowers continue to produce exploitable amounts of nectar, a bird has the best probability of finding food in a given plant if it feeds at a time of day when visits from other species are least frequent. Territorial birds can actively limit visits from other individuals during preferred times. If nectar availability declines through the day, however, territorial exploitation of a clump may become unprofitable, such that energetic expense of foraging and defending is less than energy loss incurred through ignoring the clump (see Schoener 1974c). Therefore, territorial birds may control clumps for part of the day only. Trapliners or other birds that can profitably exploit less rich resources may then utilize the same flowers. Thus, diurnal changes in nectar production or in visits from certain birds may result in diurnal flower selection differences among hummingbird species, and time-dependent aggression may amplify these differences.

Diurnal partitioning sometimes occurred at low-density plants that attracted two or more species, but occurred most consistently at high flower densities. High-density *Hamelia* shrubs, whose heavily exploited flowers often lacked nectar later in the day, usually supported static territories of *Amazilia* or other species such as *A. tzacatl* from dawn through at least midmorning but were sometimes abandoned to *Chlorostilbon* later in the day (Table 6a). Several species, especially *Philodice*, often visited high-density *Inga* during the hour or so after dawn before *Amazilia* set up territories, and concentrated later visits at times when *Amazilia* activity was lowest (see Colwell 1973 for a similar case involving *Colibri* and *Eugenes fulgens*). Table 6a presents a slightly different situation: an *Amazilia*, a *Eupherusa* male, and a *Lampornis* male successively defended the tree observed. Less differentiation was observed at high-density *Lobelia*: *Philodice* often concentrated visits early in the day, *Colibri* at dusk, but *Chlorostilbon*, *Hylocharis*, and *Amazilia* often fed throughout the day. The average *Lobelia* flower in a high density received only 0.86 visits per day, however (Table 1). The Poisson distribution predicts that if all hummingbirds foraged randomly only 58% of the flowers would receive any visits during the day; only 21% would receive more than one visit; and only 5% would receive two or more visits within the same hour. *Lobelia* flowers produced nectar throughout the day (Fig. 5c), and a bird visiting a given flower more than an hour after a previous visit would probably encounter exploitable amounts of nectar. Thus nectar in high-density *Lobelia* patches was effectively

TABLE 7. Example of partitioning in the seasonal dimension. Data for all observations at high-density *Inga brenesii* trees. First figure per cell: number of flowers visited during 7-h (June–October) or 12-h (November–December) observation periods. Figure in parentheses: utilization of this resource state by hummingbird population (see Eq. 2, Table 8). Decimal:  $q_{irm}$  or proportion of  $i$ 's total utilization of this biotic resource state occurring in month  $m$

Bird species ( $i$ )	Month ( $m$ )						
	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Amazilia</i>	1638 (2,161.4) .0366	534 (2,297.8) .0389	281 (3,641.4) .0616	1178 (14,425.9) .2441	1513 (19,273.5) .3261	2550 (13,106.9) .2218	2917 (4,196.4) .0710
<i>Philodice</i>				453 (5,547.5) .1560	1746 (22,241.6) .6254	1250 (6,424.9) .1807	939 (1,350.8) .0380
<i>Colibri thalassinus</i>	101 (133.3) .0318				83 (1,057.3) .2525	579 (2,976.0) .7108	14 (20.1) .0048
<i>Hylocharis</i>					26 (331.2) 1.0		
<i>Archilochus</i>						447 (2,297.6) 1.0	
<i>Eupherusa</i>	30 (39.6) .0217	278 (1,196.2) .6529			31 (394.9) .2169	37 (190.2) .1045	
<i>Campylopterus</i>					18 (229.3) 1.0		
<i>Lampornis</i>	14 (18.5) .0012	1,078 (4,638.6) .2991			852 (10,853.3) .6997		
<i>Elvira</i>	5 (6.6) .0050					166 (853.3) .6471	319 (458.9) .3840
<i>Colibri delphinae</i>					94 (1,197.4) 1.0		

superabundant, and great divergence among diurnal foraging patterns would have been superfluous.

#### Partitioning in the seasonal dimension

Hummingbirds appearing in a community at different times of the year encounter different dispersions of nectar supplies among the flowering plant species. Due to changes in numbers or simply in foraging patterns, the relative impacts of different hummingbird populations on a single biotic resource state may change asynchronously from month to month. The result is a partitioning of that biotic resource state along a seasonal dimension, with the biotic resource state providing distinct "seasonal resource states" in different months. The species foraging at high-density *Inga* trees provided an exemplary case of divergence in seasonal foraging intensity (Table 7).

#### Partitioning in the arthropod dimension

The arthropods eaten by hummingbirds can be considered a dimension containing at least three distinct resource states: arthropods in flower corollas, foliage arthropods, and aerial arthropods. Edible arthropods living within flower corollas were par-

titioned along with nectar supplies as described above. Territorial birds, skillful fliers that expend much energy while hovering (cf. Feinsinger and Chaplin 1975), caught aerial arthropods by sallying from perches, while nonterritorial birds, generally slower fliers that can hover with less energetic expense (Feinsinger and Chaplin 1975), exploited foliage arthropods (Table 2). Unless exploitable flowers are very limited or irregular (see Wagner 1946; Wolf 1970), however, arthropods only provide diet supplements for hummingbirds and do not serve as a primary food source. In Monteverde, where numbers of exploitable flowers were always available (Fig. 6), hummingbirds fed foliage and aerial arthropods to nestlings (P. Feinsinger, *personal observations*; see Skutch 1967) but otherwise exploited these resource states only sporadically. Therefore, foliage and aerial arthropods were apparently an unlimited and nonlimiting alternate food source that scarcely affected interactions between hummingbird species. Except for corolla-inhabiting arthropods, which constitute floral resources operationally equivalent to nectar, the arthropod dimension will not be considered in the analyses below.

## THE ANALYSIS OF FEEDING ECOLOGY

**The unit of analysis.**—To move from observations on foraging patterns within the various dimensions to statements about relative population size, niche breadth, and niche overlap, one needs measures of resource availability and resource use. The amount of resource available on a particular plant is roughly proportional to the number of flowers the plant possesses, and the amount of resource a visiting hummingbird uses is proportional to the number of flowers visited. Interspecific differences in mean nectar production per flower (Table 2) suggest weighting. Nectar available varies greatly with the individual flower (P. Feinsinger, *personal observation*), time of day (Fig. 5), and previous visit pattern (which also varies with plant species, but not in a predictable manner), however, such that mean nectar production may not be correlated with nectar availability. Furthermore, nectar quality also varies widely, not only with plant species (Baker 1975) but also with time of day and weather conditions (P. Feinsinger, *personal observations*; see Oertel 1946). I could conceive of no practical weighting statistic to correct for the among-species, let alone the among-flower, variation. Therefore, I shall consider the individual flower, without any weighting, as the operational resource unit.

**Utilization of biotic resource states.**—The resource quantity available within a particular biotic resource state  $r$  during month  $m$  is then the number of flowers on all plants of  $r$  in the study habitats at the midpoint of  $m$ , of  $F_{rm}$ . Similarly, utilization ( $U$ ) of  $r$  by a particular hummingbird population  $i$  during month  $m$  is proportional to the total number of flowers visited by that population on the average day. To estimate utilization, I assumed that the visits to the flowers on the plant(s) observed represented the pattern of visits to all flowers in that biotic resource state that day. I occasionally observed two different plants of a particular biotic resource state within the same month, and the resulting similarities in data indicated that this assumption was justified. Then the utilization of biotic resource state  $r$  by population  $i$  on a given day in month  $m$ ,  $U_{irm}$ , is the number of  $r$  flowers that birds of species  $i$  visit during the observation period, corrected to a 12-h basis if necessary, times the ratio of  $F_{rm}$  to the number of flowers available on the plant(s) observed (Eq. 2, Table 8). For example, utilization figures for July 1972 (Table 4) are simply the raw observation figures multiplied by the ratio 12/7 and then by the ratio of flowers on plots to flowers observed for each biotic resource state. Similarly, utilization figures for high-density *Inga* in each month (Table 7) are simply the observed numbers of flowers visited by each species corrected from 7- to 12-h values

where necessary (June–October) and then multiplied by the ratio of high-density *Inga* flowers available at the midpoint of that month (cf. Fig. 4b) to the number in the tree observed. All further analyses are based on these monthly utilization figures (presented in Feinsinger 1974).

**Effective populations and diversity.**—The total number of flowers that species  $i$  visits in a given day, or simply  $U_{i\cdot m}$ , estimates the effective population of  $i$  in the study habitats (Eq. 3). The guild effective population is then  $U_{\cdot m}$  (Eq. 4). For instance, the effective population of *Amazilia* in July 1972 was the sum of *Amazilia* utilization figures for individual biotic resource states, or 6,205.7 (Table 4); the guild effective population was 14,229.0. Effective population best measures the impact of each species  $i$  on the guild's resource spectrum. It might be argued that this measure bears no relation to the actual number of birds present; for example, the same number of birds might need to forage among many more *Inga* than *Lobelia* flowers, creating an inflated value for effective population when concentrating on the former. Nevertheless, Spearman rank correlations of the core species' effective populations with the 14 2-mo rolling averages of the numbers counted in end-of-month hummingbird censuses were significantly positive (one-tailed tests):  $r_s = .4989, p < .05$  (*Amazilia*);  $r_s = .8208, p < .001$  (*Chlorostilbon*);  $r_s = .6978, p < .01$  (*Philodice*);  $r_s = .6636, p < .01$  (*Colibri*).

The total annual effective population of species  $i$  is then proportional to the 12-mo sum of the effective populations, or  $U_{i\cdot}$  (Eq. 5; data presented in Feinsinger 1974).

Hummingbird species diversity in month  $m$  ( $D_{Hm}$ ), like flower diversity, is calculated with the inverse Simpson index (Eq. 6). This measure incorporated simple hummingbird species richness ( $S_m$ ) quite well: over 14 mo,  $r_s = .7079 (p < .01)$ .

**Niche breadths: Monthly values.**—Niche breadth of  $i$  in month  $m$  (Eq. 7) is simply the diversity of flowers visited by  $i$  (see Levins 1968). Niche breadth varies from one, for a population visiting one biotic resource state, to  $R_m$ , for a population making equal numbers of visits to all  $R_m$  biotic resource states. Each month's guild niche breadth (Eq. 8) is the mean of all species' niche breadths, each weighted by that species' effective population.

**Niche breadth: Annual values.**—Mean niche breadth of population  $i$  (Eq. 9) is calculated over those months, May 1972–April 1973 inclusive, that  $i$  was present. Circannual niche breadth of  $i$  (Eq. 10) is instead based on  $p_{ir\cdot}$ , or the ratio of  $i$ 's total use of each biotic resource state during the last 12 mo of the study ( $U_{ir\cdot}$ ) to its annual effective population.

TABLE 8. Terms used in analysis

Number	Term	Equation
(2)	Utilization of resource state by hummingbird population <sup>1</sup>	$U_{irm} = V_{irm}(F_{rm}/A_{rm})$
(3)	Effective population <sup>2</sup>	$U_{i\cdot m} = \sum_{r=1}^{R_m} U_{irm}$
(4)	Guild effective population <sup>3</sup>	$U_{\cdot\cdot m} = \sum_{i=1}^{S_m} U_{i\cdot m}$
(5)	Annual effective population <sup>4</sup>	$U_{i..} = \sum_{m=1}^M U_{i\cdot m}$
(6)	Hummingbird species diversity <sup>5</sup>	$D_{Hm} = 1 / \sum_{i=1}^{S_m} p_{i\cdot m}^2$
(7)	Niche breadth <sup>6</sup>	$B_{im} = 1 / \sum_{r=1}^{R_m} p_{irm}^2$
(8)	Guild niche breadth	$B_{im} = \sum_{i=1}^{S_m} (B_{im} U_{i\cdot m}) / U_{\cdot\cdot m}$
(9)	Mean niche breadth	$B_{i\bar{m}} = \sum_{m=1}^M B_{im} / M$
(10)	Circannual niche breadth <sup>7</sup>	$B_{i\cdot} = 1 / \sum_{r=1}^{R_i} p_{ir}^2$
(11)	Gross niche overlap between two species <sup>8</sup>	$G_{(ij)m} = \sum_{r=1}^{R_m} \min(p_{irm}, p_{jrm})$
(12)	Spatial overlap <sup>9</sup>	$K_{(ij)rm} = \sum_{k=1}^4 \min(p_{ik}, p_{jk})$
(13)	Diurnal overlap <sup>10</sup>	$T_{(ij)rm} = \sum_{h=1}^H \min(p_{ih}, p_{jh})$
(14)	Within-plant overlap	$O_{(ij)rm} = (K_{(ij)rm})(T_{(ij)rm})$
(15)	Adjusted niche overlap between two species	$A_{(ij)m} = \sum_{r=1}^{R_m} \{\min(p_{irm}, p_{jrm})\} \{O_{(ij)rm}\}$
(16)	Gross niche overlap of species <sup>11</sup>	$G_{(ij)\bar{m}} = \sum_{r=1}^{R_m} \min(p_{irm}, p_{jrm})$
(17)	Adjusted niche overlap of species <sup>12</sup>	$A_{(ij)\bar{m}} = \sum_{r=1}^{R_m} \{\min(p_{irm}, p_{jrm})\} \{O_{(ij)\bar{m}}\}$
(18)	Guild gross niche overlap	$G_{(\bar{i}\bar{j})m} = \sum_{i=1}^{S_m} G_{(ij)m} U_{i\cdot m} / U_{\cdot\cdot m}$
(19)	Guild adjusted niche overlap	$A_{(\bar{i}\bar{j})m} = \sum_{i=1}^{S_m} A_{(ij)m} U_{i\cdot m} / U_{\cdot\cdot m}$
(20)	Mean gross niche overlap between two species <sup>13</sup>	$G_{(ij)\bar{m}} = \sum_{m=1}^M G_{(ij)\bar{m}} / M$

TABLE 8. Continued

Number	Term	Equation
(21)	Mean adjusted niche overlap between two species	$A_{(ij)\bar{m}} = \sum_{m=1}^M A_{(ij)m} / M$
(22)	Gross circannual niche overlap between two species <sup>14</sup>	$G_{(ij).} = \sum_{r=1}^R \min(p_{ir.}, p_{jr.})$
(23)	Gross circannual niche overlap of species <sup>15</sup>	$G_{(i\bar{j}).} = \sum_{r=1}^R \min(p_{ir.}, p_{jr.})$
(24)	Seasonal overlap between two species <sup>16</sup>	$M_{(ij)r} = \sum_{m=1}^{12} \min(q_{irm}, q_{jrm})$
(25)	Seasonal overlap of species <sup>17</sup>	$M_{(i\bar{j})r} = \sum_{m=1}^{12} \min(q_{irm}, q_{jrm})$
(26)	Circannual within-state overlap between two species	$O_{(ij)r.} = \sum_{m=1}^{12} \{\min(q_{irm}, q_{jrm})\} \{O_{(ij)rm}\}$
(27)	Circannual within-state overlap of species <sup>18</sup>	$O_{(i\bar{j})r.} = \sum_{m=1}^{12} \{\min(q_{irm}, q_{jrm})\} \{O_{(i\bar{j})rm}\}$
(28)	Circannual niche overlap between two species	$A_{(ij).} = \sum_{r=1}^R \{\min(p_{ir.}, p_{jr.})\} \{O_{(ij)r.}\}$
(29)	Circannual niche overlap of species	$A_{(i\bar{j}).} = \sum_{r=1}^R \{\min(p_{ir.}, p_{jr.})\} \{O_{(i\bar{j})r.}\}$

<sup>1</sup>  $i$  = hummingbird species;  $r$  = resource state;  $m$  = month;  $V$  = flowers visited on observed plant(s);  $A$  = flowers available on observed plant(s);  $F_{rm}$  = number of flowers available on all plants of  $r$  at midpoint of  $m$ .

<sup>2</sup>  $R_m$  = total number of resource states available in month  $m$ .

<sup>3</sup>  $S_m$  = total number of hummingbird species present in month  $m$ .

<sup>4</sup>  $M$  = number of months species  $i$  present in community, May 1972–April 1973 inclusive.

<sup>5</sup>  $p_{i..m} = U_{i..m} / U_{..m}$ .

<sup>6</sup>  $p_{irm} = U_{irm} / U_{i..m}$ .

<sup>7</sup>  $p_{ir.} = U_{ir.} / U_{i..}$ , where  $U_{ir.} = \sum_{m=1}^M U_{irm}$ ;  $R$  = total number of resource states (19).

<sup>8</sup>  $j$  = second hummingbird species.

<sup>9</sup>  $p_{ik}$  = proportion of  $i$ 's visits to flowers in spatial resource state  $k$ .

<sup>10</sup>  $p_{ih}$  = proportion of  $i$ 's visits made in diurnal resource state  $h$ ;  $H = 6$  or 7.

<sup>11</sup>  $p_{-rm} = (U_{.rm} - U_{irm}) / (U_{..m} - U_{i..m})$

<sup>12</sup>  $O_{(ij)rm}$  obtained in same fashion as  $O_{(ij)rm}$  if within-plant overlap between  $i$  and all other species is significant.

<sup>13</sup>  $M$  = number of months both  $i$  and  $j$  present.

<sup>14</sup>  $p_{ir.} = U_{ir.} / U_{i..}$ , for May 1972–April 1973 inclusive.

<sup>15</sup>  $p_{jr.} = (U_{.r.} - U_{ir.}) / (U_{..} - U_{i..})$ .

<sup>16</sup>  $q_{irm} = U_{irm} / U_{ir.}$ .

<sup>17</sup>  $q_{jrm} = (U_{.rm} - U_{irm}) / (U_{.r.} - U_{ir.})$ .

**Niche overlaps: Monthly values.**—The sample similarity measure, which compares the distribution of  $a$  and  $b$  over  $C$  conditions, is the simplest and most intuitively obvious measure of niche overlap (Colwell and Futuyma 1971):

$$\text{Similarity} = 1 - \frac{1}{2} \sum_{c=1}^C |p_{ac} - p_{bc}|$$

$$= \sum_{c=1}^C \min(p_{ac}, p_{bc}).$$

Similarity varies from zero (no similarity) to one (identity). Then gross niche overlap between hummingbird species  $i$  and  $j$  in month  $m$  (Eq. 11) is calculated as the similarity between their utilization patterns over biotic resource states. For instance,

gross niche overlap between *Amazilia* and *Chlorostilbon* in July 1972 (Table 4) was .0762 (high-density *Hamelia*) + .0044 (low-density *Hamelia*), or .0806. Similarly, gross niche overlap between *Euperusa* and *Lampronis*, both feeding exclusively on high-density *Inga*, was 1.0.

Based solely upon partitioning in the plant dimension, gross niche overlap does not take into account within-plant partitioning in spatial and diurnal dimensions. Therefore, it does not truly estimate the similarity between the resource exploitation patterns of populations *i* and *j*, their actual niche overlaps. We may approximate this actual niche overlap by calculating a value that is corrected for within-plant overlap.

Significant within-plant partitioning by species *i* and *j* was arbitrarily said to have occurred if and only if *i* and *j* had each made at least three foraging bouts, totalling at least 35 flowers probed, during the observation period and statistical tests applied to these raw data indicated significant interspecific differences at the 1% level. I tested for spatial partitioning by calculating chi-squared values for the distributions of flowers probed over the four spatial resource states, and tested for temporal partitioning by calculating Kolmogorov-Smirnov two-sample values (see Siegel 1956) for the distributions of flowers probed over seven 1-h intervals (wet season) or six 2-h intervals (dry season). For example, in November 1972, *Amazilia* and *Philodice* spatially partitioned the resources in the observed high-density *Inga* (Table 5):  $X^2 = 842$ ,  $p < .001$ . *Chlorostilbon* and *A. tzacatl* diurnally partitioned the resources in the high-density *Hamelia* shrub in June 1972 (Table 6); the Kolmogorov-Smirnov statistic was highly significant ( $p < .001$ ).

When statistically significant spatial partitioning within a plant of biotic resource state *r* in month *m* is demonstrated, then spatial overlap is calculated with the similarity measure (Eq. 12). For instance, spatial overlap between *Amazilia* and *Philodice* on *Inga* in November 1972 (Table 5) was .3847 (top outside) + 0 (top inside) + .1920 (lower outside) + 0 (lower inside) = .5767. Diurnal overlap is calculated similarly (Eq. 13). For instance, diurnal overlap between *A. tzacatl* and *Chlorostilbon* at the high-density *Hamelia* shrub in June 1972 (Table 6a) was .0384 (0500–0600) + .2070 (0600–0700) + .0321 (0700–0800) + 0 (remaining hours) = .2775. If the plant is both spatially and diurnally partitioned, within-plant overlap (Eq. 14) is the product of the two values. If species *i* and *j* fail to partition the plant, then within-plant overlap is, of course, one. I assumed that the within-plant overlap observed on a single plant or plant clump applied to all plants of that biotic resource state in that month. Again, data from replicate observations indicated that within-

plant overlap values at plants of a given biotic resource state remained roughly the same within a given month despite variation in the precise pattern of flower visits. Thus, to obtain the adjusted niche overlap between populations *i* and *j* in month *m*, (Eq. 15), the *r*th term of the formula for gross niche overlap is weighted by within-plant overlap for *r*. For instance, adjusted niche overlap between *Amazilia* and *Chlorostilbon* in July 1972 (Table 4) was calculated as follows: temporal overlap on high-density *Hamelia* was .4648; spatial overlap on the same was .6513; thus within-plant overlap was .3027. The only other jointly visited plant, low-density *Hamelia*, was not significantly partitioned; within-plant overlap was simply one. Therefore, adjusted niche overlap was (.0762)(.3027) + (.0044)(1.0) = .0253.

Each population's niche, however, overlapped not one but several other hummingbird niches. Overlap of population *i* with all other populations *j*, hereafter termed "overlap of *i*" as opposed to "overlap between *i* and *j*," is more significant to the feeding ecology of *i* than overlap between *i* and each *j* separately. Gross and adjusted niche overlaps of *i* (Eq. 16, 17) are obtained by comparing *i*'s exploitation pattern with summed exploitation patterns of all other populations present. Guild gross niche overlap (Eq. 18) and guild adjusted niche overlap (Eq. 19) are calculated as weighted means of these values for all species present.

*Niche overlaps: Annual values.*—Mean gross niche overlap between populations *i* and *j* for those months when both were present, May 1972–April 1973 inclusive, is the arithmetic mean of gross niche overlaps for those months (Eq. 20); mean adjusted niche overlap between *i* and *j* (Eq. 21) is calculated similarly. Mean gross and adjusted niche overlaps of population *i* are means of gross and adjusted niche overlaps for those months when *i* was present.

Simple means of niche overlaps fail to incorporate partitioning in the seasonal dimension. Nor do niche overlaps calculated simply from species' annual utilization of each biotic resource state, or gross circannual niche overlaps (Eqs. 22, 23), include seasonal partitioning. To account for monthly partitioning as defined, a seasonal overlap value is calculated on each biotic resource state for each species pair (Eq. 24) or for each species and the remainder of the guild (Eq. 25). For instance, seasonal overlap between *Amazilia* and *Philodice* on high-density *Inga* (Table 7) was 0 (June–August) + .1560 (September) + .3261 (October) + .1807 (November) + .0380 (December) = .7008. To allow for the within-plant partitioning taking place each month, the seasonal overlap value is next adjusted by multiplying the *m*th term by the appropriate within-plant partitioning value (Eqs. 26, 27). This procedure gives

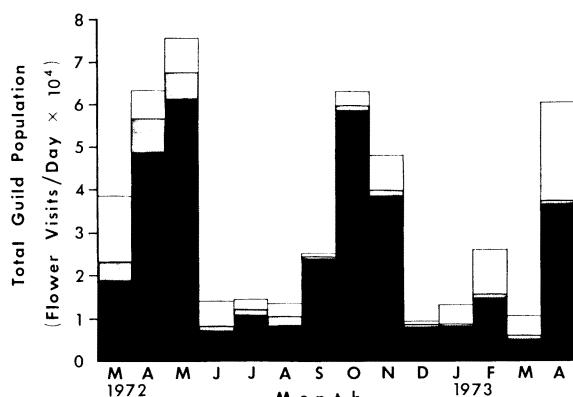


FIG. 8. Guild effective population. Solid area: territorial species only; open area: nonterritorial species only; stippled area: unclassified species.

the circannual within-state overlap on resource state  $r$ . For instance, *Amazilia* and *Philodice* feeding on high flower densities of *Inga* (Table 7) actually overlapped not .7008 but .2287, when within-plant overlaps were included (.2938 in September, .2693 in October, .4458 in November, .3821 in December):  $(.1560)(.2938) + (.3261)(.2693) + (.1807)(.4458) + (.0380)(.3821) = .2287$ .

Then adjusted circannual niche overlap between  $i$  and  $j$  (Eq. 28) is their gross circannual niche overlap recalculated with the  $r$ th element multiplied by the circannual within-state overlap value for  $r$ . Adjusted circannual niche overlap of  $i$  by all other species (Eq. 29) is calculated similarly.

Throughout the calculation of niche overlaps I did not heed May's (1975) "awful warning" against multiplying overlap values obtained in different dimensions. Ideally, each intersection of two or more dimensions—e.g., a given region of an *Inga* tree during a particular 2-h time period in a particular month—should be treated as a unique resource state, and adjusted overlaps should be calculated from species' joint distributions over all such resource states. Attempts at calculating within-plant partitioning values in such fashion (each cell = number of flowers visited by  $i$  in area  $k$  during time period  $h$ ) often yielded cell values too small for tests of significance. Overlaps calculated from these cells were biased toward underestimation. Calculation of circannual overlap values following May's advice also became unwieldy. If resource partitioning in one dimension is not entirely independent of that in another—and I suspect that such was often the case here—then the method I used, a variation of the "product  $\alpha$ " method, may overestimate overlap (May 1975). But a product  $\alpha$  cannot underestimate overlap. Given the low overlap values that resulted from the procedure used here (high adjusted overlap

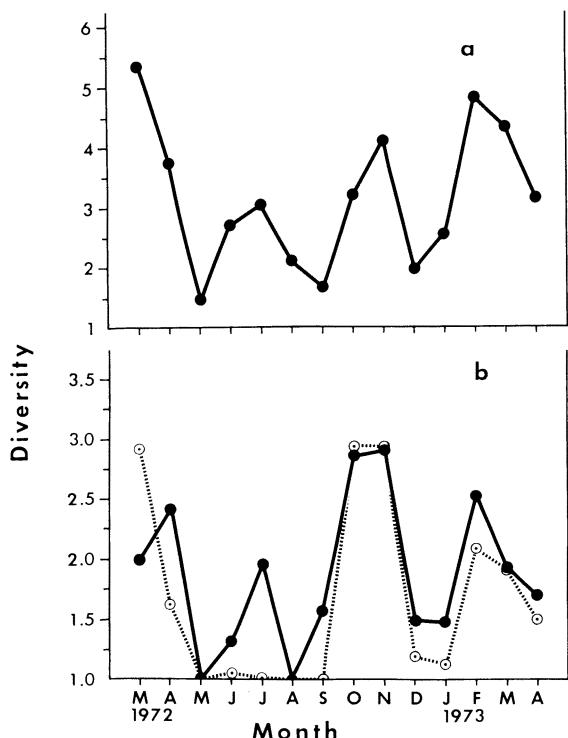


FIG. 9. Hummingbird diversity. (a) Diversity of all hummingbirds ( $D_{Hm}$ ; Eq. 6, Table 8); (b) Diversity of territorial species (solid line) and nonterritorial species (dashed line) only.

values occurred largely at times when within-plant partitioning did not occur and product  $\alpha$ s were not calculated) I did not feel that overestimation was a problem. Thus, given the available data, the values obtained from Eqs. 15, 17, 19, 28, and 29 (Table 8) are the best estimates of overall joint use of resources within the community, or actual niche overlap.

## RESULTS OF THE ANALYSIS

### The guild

Over the 14 mo, the guild effective population ranged from  $< 10,000$  flowers visited per day to  $> 75,000$  (Fig. 8). The dispersion of these visits among hummingbird species also varied, generating marked changes in hummingbird species diversity (Fig. 9). Guild niche breadth fluctuated from near 1.0 (most birds concentrating on a single biotic resource state) to nearly 3.0 (Fig. 10). Gross and adjusted niche overlap ranged from  $< 10\%$  in some months to 80% in others (Fig. 11).

Most temporal shifts in these values were linked to changes in the resource spectrum. Despite the abundant *Lobelia* flowers available in March 1972 (cf. Fig. 4c), however, a diversity of biotic resource states received visits from the diverse hummingbirds

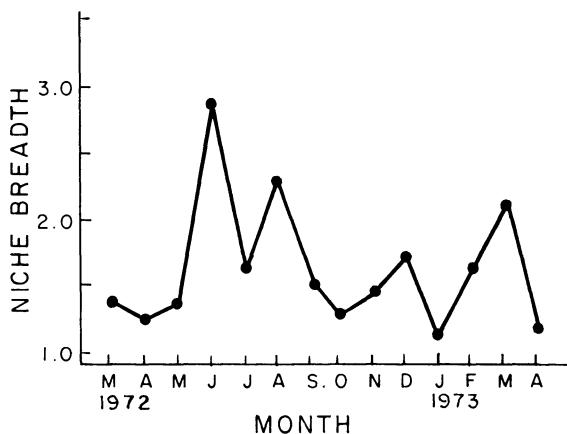


FIG. 10. Guild niche breadth (Eq. 8, Table 8).

present (Fig. 9). In April, though the resource base had changed only slightly, most birds converged upon the fields of *Lobelia*. Thus, from March to April the effective population increased (Fig. 8), both measures of niche overlap increased (Fig. 11), and guild niche breadth shrank (Fig. 10). In May, an influx of *Amazilia* juveniles dominated the high-density *Lobelia* still available (Fig. 9). The few other populations remaining diverged onto other biotic resource states, and guild niche overlap declined (Fig. 11).

From June through August 1972, the resource base included low numbers but a high diversity of flowers (Figs. 6, 7). Some high-density *Inga* and *Hamelia*, plus a number of low-density resources, were available. *Amazilia* and other territorial species easily defended the more attractive resource clumps, while excluded species such as *Chlorostilbon* exploited undefended plants. Therefore, guild niche overlaps

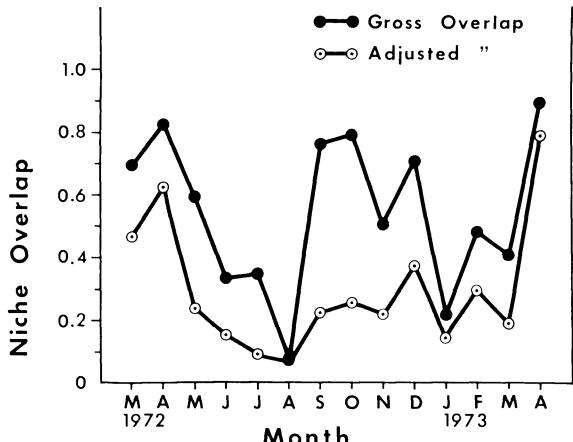


FIG. 11. Guild niche overlaps (Eqs. 18 and 19, Table 8). Compare with Figs. 4, 6.

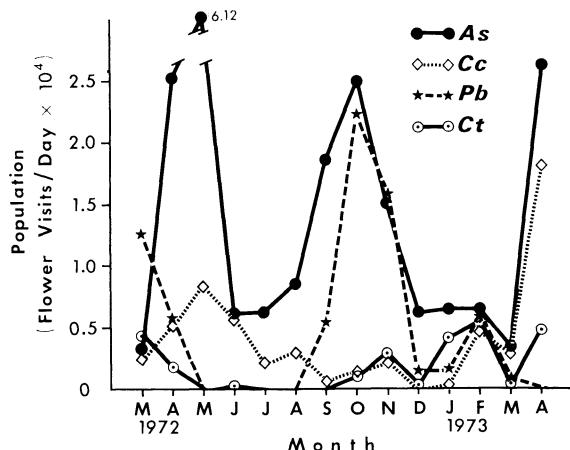
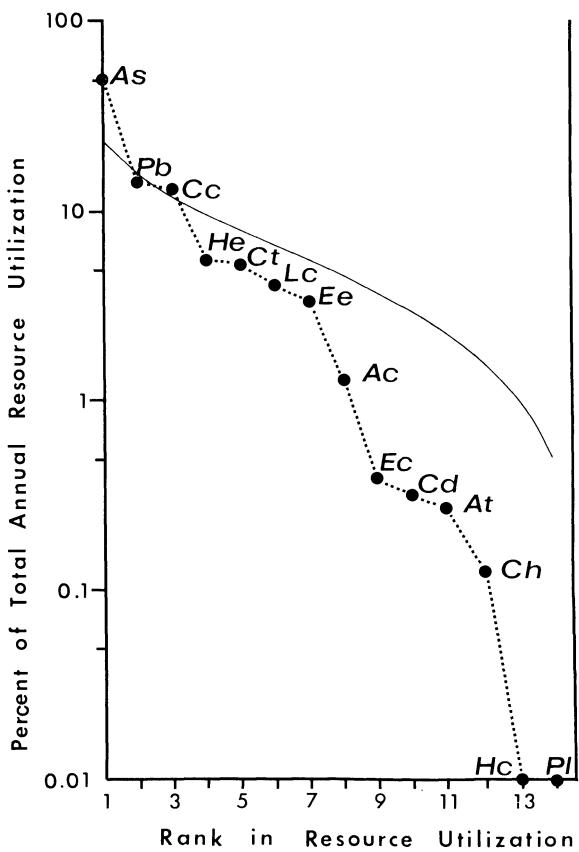
FIG. 12. Effective populations, core species. As: *Amazilia*; Cc: *Chlorostilbon*; Pb: *Philodice*; Ct: *Colibri*.FIG. 13. Annual dominance-diversity curve. Ordinate: contribution of species  $i$  to annual guild effective population, May 1972–April 1973 inclusive ( $U_i / \sum U_j$ ); abscissa: rank of species  $i$  in annual effective population (see Eq. 5, Table 8). Solid line is curve predicted by MacArthur "broken-stick" model for 14 species (see Whittaker 1970). For abbreviations see Table 2.

TABLE 9. Mean niche breadth (Eq. 9, Table 8), circannual niche breadth (Eq. 10), mean niche overlap, and circannual niche overlaps (Eqs. 23, 29) for each core species and two peripheral species having widely different impacts

Parameter	Species					
	<i>Amazilia</i>	<i>Chlorostilbon</i>	<i>Philodice</i>	<i>Colibri</i>	<i>Hylocharis</i>	<i>Heliomaster</i>
Mean niche breadth	1.6579	2.2493	1.5418	1.3773	1.1910	1.0000
Circannual niche breadth	3.2928	3.1815	1.9611	3.0515	2.0092	1.0000
Mean gross niche overlap	.4842	.3144	.7067	.4855	.6093	.000012
Mean adjusted niche overlap	.2477	.1777	.3039	.2436	.5308	.000012
Gross circannual niche overlap	.7872	.5265	.4938	.6137	.5249	.000002
Adjusted circannual niche overlap	.2132	.1852	.1112	.1345	.1795	.000001

remained low (Fig. 11), and niche breadth generally stayed high (Fig. 10).

From September through November, many *Inga* produced high flower densities (Fig. 4b). Guild effective population (Fig. 8) and gross overlap (Fig. 11) increased, while hummingbird diversity (Fig. 9) and guild niche breadth (Fig. 10) declined. Birds exploited *Inga* in divergent spatial and diurnal fashions, however, and guild adjusted overlap rose only slightly. Equating *Inga* flowers to more copious nectar-producers may have led to underestimates of niche breadth values for those months but overestimates, if anything, of niche overlaps. Estimates of effective populations could have been inflated likewise; independent estimates of population increases during those months, however, agree well with the increases in the effective population estimate. In December, as *Inga* flowers declined in abundance (Fig. 4b), the numbers and diversity of hummingbirds also fell.

No high flower densities existed during January 1973. A low but diverse effective population (Figs. 8, 9) partitioned the low-density resources along the plant dimension, and niche overlap fell (Fig. 11). In February, as *Lobelia* flowers began to dominate the resource base (Fig. 4c), several populations again focused on them (Figs. 8, 9). The contrast between March, when the hummingbirds practically ignored the abundant *Lobelia* of Plot O, and April, when hummingbirds swarmed to these flowers, repeated the pattern of March–April 1972. Adjusted overlap jumped from 19% to a record high of almost 80% (Fig. 11).

#### The individual species

Shifts in guild foraging structure only reflected changes in feeding patterns among the individual species. Despite the subjectivity of my distinction between core and peripheral species, I feel that the

results of the analysis are in fact more directly relevant to the core species as defined, and I shall concentrate on them below.

*Amazilia*.—Continuously present, the principal territorial species led the guild in effective population during all but 2 mo and clearly led in annual effective population (Fig. 13). Therefore, the month-to-month shifts in guild values discussed above were greatly influenced by changes in the *Amazilia* population (Fig. 12), niche breadth (Fig. 14), and niche overlap (Fig. 15). For example, within-plant partitioning between *Amazilia* and other species visiting *Inga* allowed *Amazilia*, and thus the guild on the average, a much lower adjusted niche overlap in September–November than in March–April 1972 and April 1973, when many *Amazilia* exploited high-density *Lobelia*. March–April changes in 1973, particularly the increase in effective population (Fig. 12), paralleled those in March–April 1972.

The *Amazilia* population concentrated on particular rich, attractive biotic resource states at particular times but exploited several over the year. Thus circannual niche breadth exceeded mean niche breadth and in fact exceeded the circannual value for any other core species (Table 9). Gross circannual niche overlap of *Amazilia* approached 80%, but partitioning along seasonal and within-plant dimensions reduced the actual overlap faced by this population to 21%. Nevertheless, this overlap value surpassed that faced by any other core species.

*Chlorostilbon*.—From May through November 1972, *Amazilia* excluded *Chlorostilbon* from certain plants entirely, and from other plants at certain temporal resource states. The traplining *Chlorostilbon* maintained a moderate effective population (Fig. 12), a low niche overlap with other populations (Fig. 15), and a broad niche (Fig. 14). During times of both 1972 and 1973 when this species could exploit

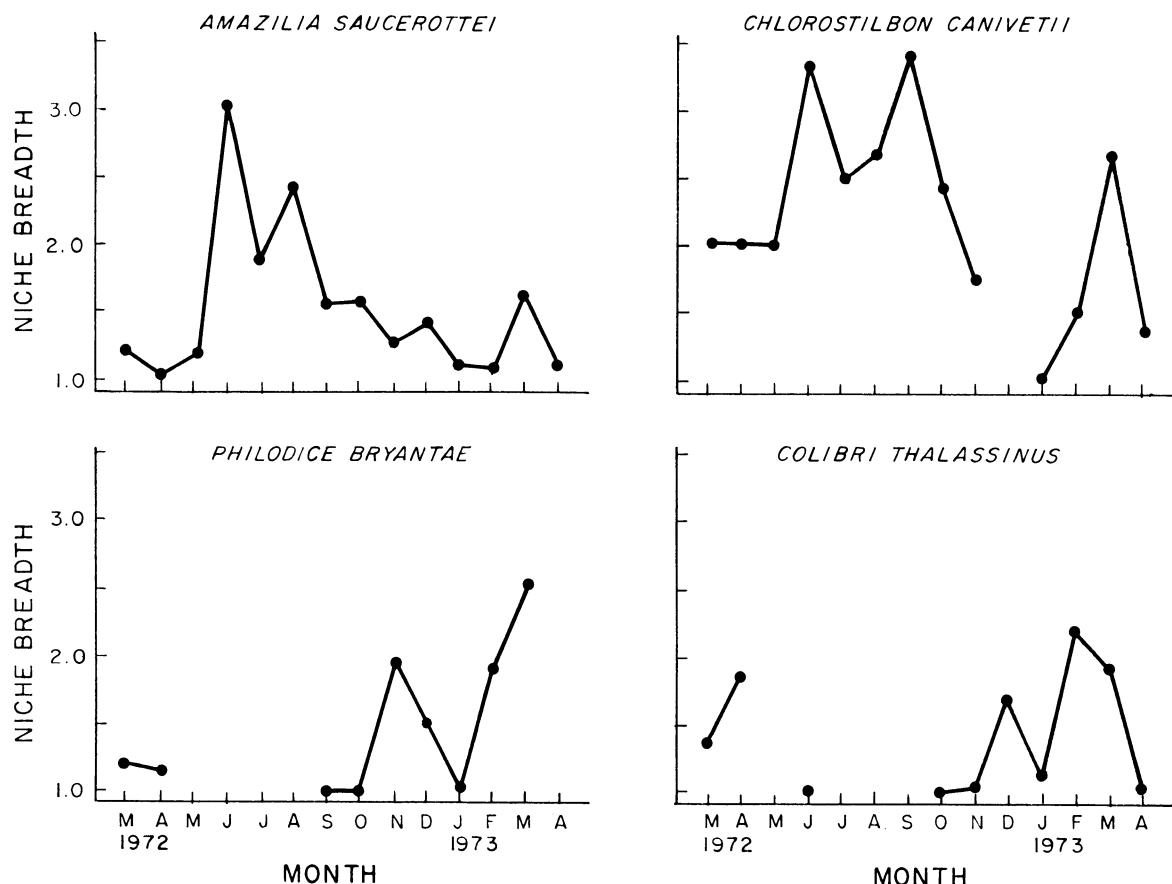


FIG. 14. Niche breadths, core species (Eq. 7, Table 8).

high-density *Lobelia*, however, overlap of *Chlorostilbon* by all other populations (Fig. 15), and overlap between this species and *Amazilia* (Fig. 16a), increased drastically.

On the average, then, *Chlorostilbon* maintained a broader niche than any other core species (Table 9). The same explosions onto high-density *Lobelia* that led to a high annual effective population (Fig. 13), however, induced a circannual niche breadth lower than that of *Amazilia*. In general, *Chlorostilbon* was successful in partitioning resources along within-plant and seasonal dimension; adjusted circannual overlaps with *Amazilia* and with the remainder of the guild were below 20% (Table 9).

*Philodice*.—This species specialized on three biotic resource states: high and low densities of *Inga* and, less consistently, high-density *Lobelia*. In two months, *Philodice* actually led the guild in importance, and was second only to *Amazilia* overall (Fig. 13). The *Philodice* effective population (Fig. 12) chiefly reflected the availability of *Inga* flowers (Fig. 4b), and circannual niche breadth was the lowest of any core member (Table 9). Since these birds could not de-

fend the popular plants they exploited against other species, their gross overlap was consistently high (Fig. 15), averaging > 70% (Table 9). Nevertheless, because *Philodice* exploited within-plant resource states differently from other species, adjusted overlap averaged only 30%. Overlap with *Amazilia*, which often selected the same plants, followed a similar pattern (Fig. 16b; Table 10). Overlap with *Chlorostilbon* occurred only in November 1972, when both species visited low-density *Inga* but fed at different times of the day, and in months when both exploited high-density *Lobelia*, on which *Philodice* also fed earlier in the day (Fig. 16d). Within-plant partitioning and extensive seasonal partitioning reduced *Philodice* circannual overlap with all other populations to 11% (Table 9), reduced overlap with *Amazilia* to < 10%, and reduced overlap with *Chlorostilbon* to scarcely more than 1% (Table 10).

*Colibri*.—This species' resource exploitation pattern exhibited three phases. During March–April 1972 and February–April 1973, *Colibri* exploited both densities of *Lobelia*. Gross and adjusted niche overlap with all other populations (Fig. 15) and especially

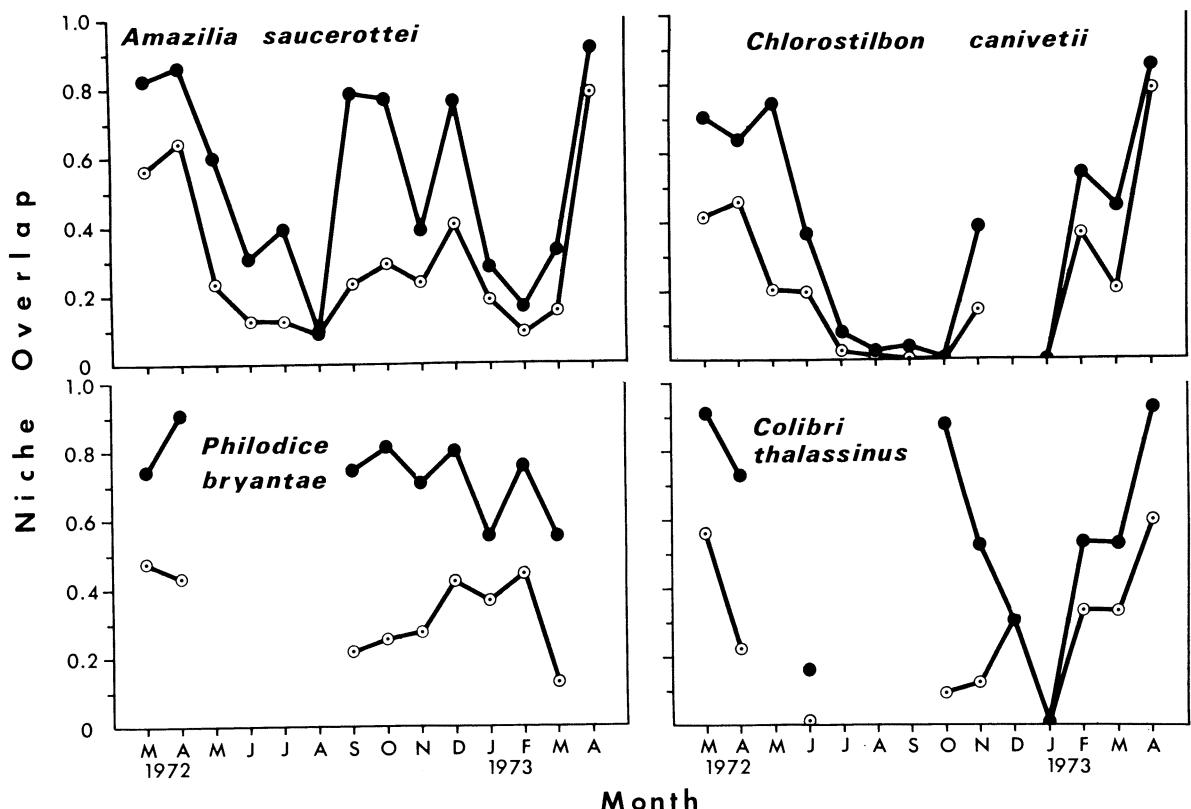


FIG. 15. Niche overlaps of core species. Overlap of each core population by all other populations (Eqs. 16 and 17, Table 8). Solid circles: gross niche overlap; open circles: adjusted overlap.

with *Chlorostilbon* (Fig. 16e) were high. During June and October–November 1972, *Colibri* concentrated on high-density *Inga* but fed at times and in areas not heavily used by other species. Therefore, though niche breadth was low (Fig. 14) and gross overlap high (Fig. 15), adjusted overlap of *Colibri* with all populations, including *Amazilia* (Fig. 16c) and *Philodice* (Fig. 16f), remained moderate. Overlap with *Chlorostilbon*, which never visited these trees, was effectively zero (Fig. 16e). During December 1972, when *Chlorostilbon* left the guild, *Colibri* effective populations also dropped. In January 1973, however, *Colibri*'s extensive traplining at low-density resources dramatically reduced overlap with other species (Figs. 15, 16).

Because this sporadic pattern never resulted in a very high effective population, *Colibri* ranked lowest of the core species in overall abundance (Fig. 13). Its mean niche breadth was also the lowest of any core species (Table 9). Mean overlap of *Colibri* resembled that of *Amazilia*. *Colibri*'s seasonal exploitation patterns resulted in considerable resource partitioning, however; adjusted circannual niche overlap was only 13%. Adjusted circannual *Colibri*–*Amazilia* and *Colibri*–*Philodice* overlaps were simi-

larly reduced to low levels (Table 10). In contrast, because both *Colibri* and *Chlorostilbon* exploited *Lobelia* so extensively, their adjusted circannual overlap of 21% exceeded that between any other pair of core species.

*Hylocharis* and *Heliomaster*.—Habitats (*sensu* Whittaker et al. 1973) of these two peripheral species impinged on the study areas to a similar extent. Niches of both species were quite narrow (Table 9). *Heliomaster* exploited only the very uncommon *Mandevilla*, while *Hylocharis* concentrated most heavily on high-density *Lobelia*. Because *Lobelia* was so abundant, *Hylocharis* ranked high in importance during several months and exceeded even *Colibri* in overall impact (Fig. 13), but *Heliomaster*'s impact was negligible. *Heliomaster*'s limited foraging pattern barely overlapped those of other populations; in contrast, *Hylocharis*' mean adjusted overlap with all populations exceeded that of any core species (Table 9). Even its adjusted circannual niche overlap, which included considerable seasonal partitioning, exceeded that of two core species (*Philodice* and *Colibri*) which were consistent guild members for much longer periods.

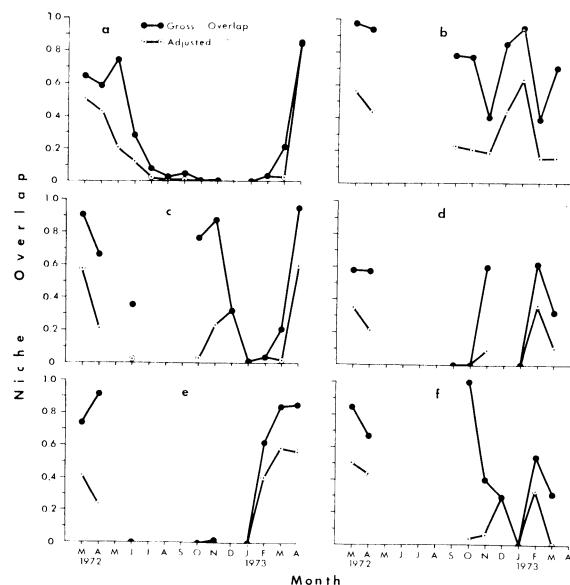


FIG. 16. Niche overlaps between core species (Eqs. 11 and 15, Table 8). (a) *Amazilia-Chlorostilbon*; (b) *Amazilia-Philodice*; (c) *Amazilia-Colibri*; (d) *Chlorostilbon-Philodice*; (e) *Chlorostilbon-Colibri*; (f) *Philodice-Colibri*. Gaps signify months when one or both species absent. Solid circles: gross overlap; open circles: adjusted overlap.

#### OVERVIEW: NICHE OVERLAPS AND COMPETITION

Thus far I have discussed the processes and results of resource partitioning without stressing the term "competition." At this point let us review the foraging patterns of the core species from the standpoint of possible competition. Following MacArthur (1972), for this purpose I shall define competition between two members of the same guild as follows: Population A exerts a competitive effect on Population B if the presence of A reduces B's potential abundance.

*Amazilia* and *Chlorostilbon*.—The virtual niche of a more specialized population may be included almost entirely within the virtual niche of a more generalized population (see reviews in Miller 1967, MacArthur 1972, Colwell and Fuentes 1975). Through interference or social dominance, the specialist population gains sole access to the niche space preferred by both (Case and Gilpin 1974, Morse 1974). The generalist, more efficient than the specialist at exploiting peripheral resources, is restricted to them. Natural absence or experimental removal of the specialist thus results in actual niche expansion of the generalist into those resource states or microhabitats previously unavailable to it (e.g., Culver 1970; see Colwell and Fuentes 1975). The interaction between *Amazilia*, the aggressive, territorial species, and *Chlorostilbon*, the subordinate,

TABLE 10. Niche overlaps between core species, annual values. a. Mean niche overlaps: first figure is mean gross niche overlap (Eq. 20, Table 8); second is mean adjusted niche overlap (Eq. 21). b. Gross circannual niche overlap (Eq. 22). c. Adjusted circannual niche overlap (Eq. 28)

Species <i>j</i>	Species <i>i</i>		
	<i>Chlorostilbon</i>	<i>Philodice</i>	<i>Colibri</i>
<b>a. Mean niche overlaps</b>			
<i>Amazilia</i>	.2062 (.1241)	.6929 (.2845)	.4405 (.1586)
<i>Chlorostilbon</i>		.2179 (.0934)	.3415 (.2223)
<i>Philodice</i>			.4529 (.1222)
<b>b. Gross circannual niche overlap</b>			
<i>Amazilia</i>	.6040	.5290	.6352
<i>Chlorostilbon</i>		.1736	.5477
<i>Philodice</i>			.2916
<b>c. Adjusted circannual niche overlap</b>			
<i>Amazilia</i>	.1715	.0958	.0988
<i>Chlorostilbon</i>		.0214	.2074
<i>Philodice</i>			.0272

traplining species, exemplifies this "included niche" model. The "sequential specialist" *Amazilia* (*sensu* Colwell 1973; see Wolf 1970), which could not profit by visiting the low-return food sources that *Chlorostilbon* regularly exploited, usurped most high-return plants or diurnal resource states that either species could have exploited. This interference normally prevented the food-limited *Chlorostilbon* population from reaching potential densities. Aside from occasional *Amazilia* lapses at high-density *Hamelia* shrubs and low-density *Inga* trees, of which the trapliners immediately took advantage, only during *Lobelia* flowering bursts was *Chlorostilbon* virtually free from *Amazilia*'s interference; its population accordingly shot up. In contrast, even in *Lobelia* fields the subordinate *Chlorostilbon* exerted little effect on the *Amazilia* population; the *Amazilia* exploiting the superabundant *Lobelia* nectar apparently limited their own numbers through excessive aggression. Thus the low *Amazilia-Chlorostilbon* actual niche overlaps in most months indicated that *Amazilia* exerted a severe competitive effect but *Chlorostilbon* did not, while high niche overlaps during *Lobelia* blooms indicated that competition was relaxed.

*Amazilia* and *Philodice*.—Two specialists can coexist (1) if their specialties do not overlap extensively (Orians and Willson 1964, Murray 1971, Cody 1974) or (2) if each limits its own population more than that of the other (Hutchinson 1958, MacArthur 1958, MacArthur and Levins 1964). Although *Amazilia* and *Philodice*, both territorial, selected the same rich plants or clumps, they foraged quite differently along within-plant dimensions and wasted little energy exploiting the same nectar supplies.

TABLE 11. The resource base and hummingbird effective populations and diversity. Pearson product-moment correlations ( $r$ ) (unless otherwise indicated) between values for months March 1972–April 1973 inclusive

Resource parameter	Guild effective population	Effective population nonterritorial birds	Effective population territorial birds	No. of hummingbird species	Hummingbird diversity <sup>a</sup>	Non-territorial hummingbird diversity <sup>a</sup>	Territorial hummingbird diversity
No. of flowers	.7221**	.3413	.6831**	.4034 <sup>b</sup>	.4473	.6221*	.5717*
No. of flowers in high densities	.7326**	.3518	.6917**			.5224	.4914
No. of flowers in low densities	.0017	.0017	.0037			.5903*	.4437
Flower diversity <sup>c</sup>	-.6416*	-.2808	-.6204*	-.0157 <sup>b</sup>	-.1472	-.2705	-.2704
Low-density flower diversity	-.1251	.2189	-.1466			-.3334	-.1688

	<i>Amazilia</i> effective population	<i>Chlorostilbon</i> effective population		<i>Philodice</i> effective population		<i>Colibri</i> effective population	
		all months	months present	all months	months present	all months	months present
No. of flowers	.3819	.2000	.1586	.5466*	.4856	.1543	-.0680
No. of flowers in high densities	.4143			.4569	.4139	.1148	-.0592
No. of flowers in low densities	-.1737	-.3471	-.2524			.2390	-.1806
Flower diversity <sup>c</sup>	-.5041	-.3128	-.2773	-.2580	-.3597	.1056	.0378
Low-density resource diversity	.0226	.4452	.3807			.2108	.3486
No. of <i>Inga</i> flowers				.8091**	.8169**		

\*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < .001$ .

<sup>a</sup>  $D_{Hm}$  (Eq. 6, Table 8).

<sup>b</sup> Spearman rank correlation coefficient.

<sup>c</sup>  $D_{Fm}$  (Eq. 1).

Possibly each population would have expanded its within-plant foraging pattern in the absence of the other (see Colwell et al. 1974). But their densities would not have increased. The resident *Philodice* of each clump interfered with other *Philodice*, while the resident *Amazilia*, unsuccessful at excluding the *Philodice*, often excluded other *Amazilia*. Thus both conditions for coexistence were fulfilled. During lean months, *Amazilia* evidently reduced nectar exploitable by *Philodice* to an unprofitable level and *Philodice* left the community. Nevertheless, when both species were present interspecific competition may have been slight despite their high gross niche overlap.

*Chlorostilbon* and *Colibri*.—Both these nonterritorial species could apparently exploit a wide range of resource species and densities. Two food-limited generalists cannot coexist, however (Miller 1967, Cody 1974). When *Chlorostilbon*, presumably the more efficient trapline, was present *Colibri* either switched strategies and exploited abundant rich re-

sources after the manner of a "sequential specialist" (see also Colwell 1973) or was absent from the community. The high overlap incurred during *Lobelia* bursts coincided with apparent low levels of competition, while in contrast low overlap during other months suggested *Chlorostilbon* interfered with *Colibri* at low-density resources and curtailed *Colibri* population size.

*Colibri* and the territorial species.—By controlling the rich resources that the more generalized *Colibri* was capable of exploiting, *Amazilia* limited the *Colibri* population as it did the *Chlorostilbon* population. Even when not excluded from rich resources, due to within-plant foraging differences *Colibri* overlapped little with either specialist (*Amazilia* or *Philodice*), and probably affected these species' resources little. Thus, actual niche overlaps were consistently low and failed to reflect shifts in competitive effects.

*Philodice* and *Chlorostilbon*.—Had *Chlorostilbon* exploited *Inga* more extensively when *Philodice* was present, its penchant for lower foliage areas may

TABLE 12. The resource base and niche breadths. Pearson product-moment correlations ( $r$ ) between values for March 1972–April 1973 inclusive, excepting months when the species was not present. No values significant

Resource parameter	Niche breadth				
	Guild	<i>Amazilia</i>	<i>Chlorostilbon</i>	<i>Philodice</i>	<i>Colibri</i>
No. of flowers	-.4506	-.5278	-.1420	.0146	.0665
No. of flowers in high densities	-.4330	-.5110	-.1051	-.0074	.0748
No. of flowers in low densities	-.1852	-.2410	-.2234	.1141	.3995
Flower diversity	.4582	.4523	-.0852	-.0167	-.0512
Low-density flower diversity	.1941	.0263	-.1934	.3927	.1378
No. of <i>Inga</i> flowers	-.1764	.0156	.1700	-.1739	-.4497
No. of <i>Lobelia</i> flowers	-.2908	-.4952	-.2266	.1347	.3965

have averted high overlap with that species. The effect of *Amazilia* on foraging patterns of both prevented even that interaction. In this case, then, a low overlap value indicated a minimal competitive effect.

*Actual resource exploitation patterns and competition.*—Field data on resource exploitation patterns can be used to interpret many aspects of feeding ecology and to explain organization within guilds, as I will attempt to do below. But the data above and other field evidence (Culver 1970, Schroder and Rosenzweig 1975) show that when interference is present it is dangerous to equate overlap values or even  $\alpha$  values calculated from these data with the magnitude of competition (Colwell and Futuyma 1971; see also Vandermeer 1972, Case and Gilpin 1974), despite protestations to the contrary (e.g., Levins 1968, Schoener 1974b). For competition relates to overlap in potential resource utilization patterns, in virtual niches, not overlap in observed patterns. Low similarity in actual resource use may indicate severe competition in some cases, insignificant competition in others.

#### THE EFFECT OF THE RESOURCE BASE UPON FEEDING ECOLOGY AND GUILD ORGANIZATION

The quantitative nature of the monthly estimates for hummingbird population size, diversity, niche breadth, and niche overlap and for resource abundance and diversity allowed statistical correlations to be drawn. These revealed how foraging patterns of individual species and the structure of the entire guild responded to general changes in the resource base.

##### Responses of effective populations

*Predictions.*—Disregarding diversity of birds and flowers, the number of flowers visited in a day by

hummingbirds (the guild effective population) should simply reflect the numbers of flowers available. Effective populations of individual species should also reflect flower numbers. Territorial birds, however, actively interfere with each other more than do nonterritorial birds. Therefore, territorial species should be less directly food-limited (Brown 1964; see MacArthur and Pianka 1966), and their responses to fluctuations in flower numbers should be less significant than the responses of nonterritorial species.

*Results.*—The size of the guild effective population correlated highly with the number of flowers available (Table 11). Nevertheless, the summed effective populations of nonterritorial species did not change consistently with changes in flower abundance. In contrast, summed effective populations of territorial species correlated highly with their food supplies; this unexpected response, contrary to predictions, is explained by the observed tendency of territorial birds to converge on the rich resource clumps most available when flowers were numerous overall.

No core species reflected flower abundance in precisely the same fashion as the entire guild. Because *Amazilia* made only sporadic visits to abundant *Lobelia* flowers in three months, response of *Amazilia* effective populations to overall changes in flower abundance was not significant. *Philodice* effective populations correlated most highly with numbers of *Inga* flowers alone. Neither the *Chlorostilbon* nor the *Colibri* population was affected significantly by overall changes in flower abundance.

##### Response of species diversity

*Predictions.*—The number of species that can coexist in a guild should reflect the diversity of resource states available (Pianka 1967; MacArthur

TABLE 13. The resource base and niche overlaps. Pearson product-moment correlations ( $r$ ) between values for months March 1972–April 1973 inclusive excepting months species  $i$  was not present. Significant values indicated as in Table 11

Resource parameter	Overlap									
	Guild		<i>Amazilia</i>		<i>Chlorostilbon</i>		<i>Philodice</i>		<i>Colibri</i>	
	Gross	Adjusted	Gross	Adjusted	Gross	Adjusted	Gross	Adjusted	Gross	Adjusted
No. of flowers	.6789*	.5811*	.6127*	.6144*	.4985	.4348	.4558	-.1062	.7812**	.2956
No. of high-density flowers			.6190*	.6238*			.4370	-.1089	.7792**	.3004
No. of low-density flowers			.3709	.2617	.2514	.1781			.1215	.2365
Flower diversity	-.7032**	-.4768	-.6989**	-.5310	-.4213	-.3486	-.3767	.3679	-.8814***	-.5616
Low-density flower diversity			-.5782*	-.3614	-.0030	-.0795			-.1607	-.0083
No. of <i>Lobelia</i> flowers	.4536	.6758*	.4476	.6471*	.7536**	.6921**	.3006	.6410	.5518	.5511

1969a, 1972; Colwell 1973). Decreased resource diversity, even with increased resource abundance, may generate lowered species diversity if a single species or a few species can best exploit the skewed resource spectrum (Patrick et al. 1954, Patrick 1968, Price 1971, Root 1973). In this study, flower diversity among biotic resource states fell as flower numbers rose. If resource base diversity were measured by flower diversity alone, hummingbird species diversity should correlate negatively with flower abundance. Flower abundance also contributes to resource diversity, however. As flowers of a single plant species increase in density, more within-plant resource states become exploitable. Heithaus (1974) found a significant positive correlation between numbers of pollinator species and flower abundance in lowland Guanacaste communities. Many authors suggest that geographical increases in resource abundance enrich species diversity (e.g., Connell and Orias 1964, MacArthur and Levins 1967, Brown 1973, Brown and Lieberman 1973). Furthermore, in the present study decreased flower diversity as measured by  $D_{fm}$  did not imply that flowers of less common species were any less available, rather that flowers of other species increased in absolute and relative numbers. Thus increased flower abundance even with decreased relative flower diversity should allow birds to employ otherwise unprofitable resource exploitation strategies in spatial and diurnal dimensions. Instead of decreased hummingbird species diversity, we should find increased species diversity.

**Results.**—Diversity of territorial species alone and of nonterritorial species alone (cf. Fig. 9b) each correlated significantly with flower numbers (Table

11). The total number of hummingbird species present ( $S_H$ ) and overall hummingbird diversity ( $D_{Hm}$ ) also correlated positively with flower numbers. These correlations were not significant, however; total  $D_{Hm}$  during *Lobelia* peaks was inordinately influenced by large territorial populations, whose diversity failed to track flower numbers, while total  $D_{Hm}$  during June–July was influenced by a rise in nonterritorial hummingbird diversity despite low flower numbers.

#### Responses of niche breadths and niche overlaps

**Predictions.**—When resources increase in abundance and decline in diversity, species should specialize on the abundant resource states (Emlen 1966, Schoener 1971, Cody 1974; see also Ward 1965). This convergence may increase gross niche overlap (Betts 1955, Nilsson 1960, Morse 1967, Root 1967, Zaret and Rand 1971, Caccamise 1974), which may be irrelevant if the resources are superabundant (cf. Hartley 1953). Conversely, when resource levels decline coexisting species should avoid overlap (Lack 1946, Ivlev 1961, Brown 1973), which may require that they contract actual niches (Root 1967, Zaret and Rand 1971, Baker and Baker 1973, Roughgarden 1974). Concurrent pressures toward less selectivity require niche expansion, however (Emlen 1966, Schoener 1971, Cody 1974), which may actually increase overlap (e.g., Erlinge 1972). Apparently, in many situations of resource stress coexisting species must choose between the perils of increased niche overlap and the perils of overspecialization. In this study, however, no such choice was necessary. In general fewer hummingbird species coexisted during the resource lows than during resource highs. Flowers

TABLE 14. The resource base and niche overlaps between the core species. Pearson product-moment correlations ( $r$ ) between values for March 1972–April 1973 inclusive, excepting months species  $i$  or  $j$  was absent. Significant values indicated as in Table 11

Resource parameter	Overlap									
	<i>Amazilia-Chlorostilbon</i>		<i>Amazilia-Philodice</i>		<i>Amazilia-Colibri</i>		<i>Chlorostilbon-Colibri</i>		<i>Philodice-Colibri</i>	
	Gross	Adjusted	Gross	Adjusted	Gross	Adjusted	Gross	Adjusted	Gross	Adjusted
No. of flowers	.4603	.4538	.1036	-.1527	.6877**	-.0724	.4494	.2222	.6691	.2431
No. of high-density flowers			.1864	-.1178	.6521*	.2628			.6537	.2538
No. of low-density flowers	.0010	.0718			.0151	.1653	.1591	.1372		
Flower diversity	-.5333	-.4703	-.1683	.2995	-.7127*	-.4701	-.5926	-.5041	-.8391**	-.0868
Low-density flower diversity	-.1252	-.0771	-.4231	-.3637	-.6726*	-.3758	.1129	.2986	-.2877	-.3647
No. of <i>Lobelia</i> flowers	.7693**	.7054**	.3475	.1986	.3113	.3711	.8790**	.6453	.2780	.5325

were more diverse relative to biotic resource states during these resource lows. Therefore, the hummingbirds remaining should have been able to decrease niche overlap and expand niches along the plant dimension simultaneously. This pattern should have held for the guild as a whole as well as for individual species. A correlation between niche breadth and flower diversity, both measured with the Simpson index and both measuring dispersion among biotic resource states, might nevertheless reveal little information (Feinsinger, *personal observation*). A population foraging haphazardly among flowers would automatically encounter relatively more flowers of a given biotic resource state (incurring a narrower niche) as that resource state became relatively more abundant (inducing a lower flower diversity). Electivity (Ivlev 1961), a better index to active selection of one resource state over another, should reveal more information: we would expect hummingbirds to select flowers of rare species less and less as other flowers became more common.

**Results: Niche breadths.**—Neither niche breadths nor selectivities followed consistent patterns. As expected, guild and *Amazilia* niche breadths contracted with increased resource abundance and expanded with increased resource diversity (Table 12), but neither trend was significant. The *Colibri* niche was broadest when *Lobelia* dominated the resource base, but *Chlorostilbon* and *Philodice* niche breadths were not consistently affected by overall changes in the resource base. Neither the guild as a whole nor any core species decreased active selection of rarer plant species as flowers increased in abundance. Three factors may explain the absence of consistent patterns. (1) Niche breadth and electivity could be

measured in only one of the several dimensions relevant to feeding ecology. (2) Neither measure is an optimal index to temporal changes in selectivity (Feinsinger *personal observation*). (3) Many studies cited above concern populations confined to a limited area, populations constant in size. Population sizes of the highly mobile hummingbirds responded flexibly to resources; though exploitation patterns of individuals might change, neither niche breadth nor selectivity of the population as a whole need change as a direct result of changes within the resource base.

**Results: Niche overlaps.**—Despite the problems associated with the niche breadth measure, as expected correlation between guild gross niche overlap and niche breadth was significantly negative ( $r = -.7355$ ,  $p < .01$ ). Guild gross niche overlap also correlated positively with flower abundance, negatively with flower diversity (Table 13). Adjusted overlap responded less significantly to overall flower abundance than to the abundance of *Lobelia* flowers. Recall that nectar in high-density *Lobelia* clumps was apparently superabundant; increased overlap reflected the birds' facultative use of effectively unlimited food supplies. Adjusted overlaps of most core species also reflected the numbers of *Lobelia* flowers (Tables 13, 14). Otherwise, however, individual overlaps followed divergent patterns.

**Effects of population size: Predictions.**—The relationships between niche parameters and resource parameters involve the avoidance of exploitation competition, here defined as "joint use of resources." Intraspecific competition in closed systems is thought to increase as populations expand (e.g., Nicholson 1948), and interspecific competition is thought to increase as populations of competitors expand (e.g.,

Park 1962). Thus many workers, invoking avoidance of competition, have attributed observed changes in niche breadths or overlaps among field populations directly to observed changes in population size. It is thought that an increasing population density forces some individuals, or the population as a whole, to exploit a broader range of habitats (Svärdson 1949) or resources (Selander 1966, Root 1967, Vandermeer 1972). This niche expansion may increase overlap with other species (e.g., Holmes and Pitelka 1968, but see Enders 1974). Conversely, negative correlations between competitor numbers and the niche or habitat breadths of particular populations have been observed (e.g., Svärdson 1949), and it is thought that increasing numbers of competitors may force a population into a narrower resource exploitation pattern (McNaughton and Wolf 1970, Colwell and Futuyma 1971, Cody 1974). If such niche contraction does not occur, overlap may increase under these conditions too (e.g., Recher 1966, Brown and Lieberman 1973).

If the species observed exploited an unchanging resource base, perhaps changes in niche breadth or overlap could be attributed to intra- and interspecific changes in population size. In most natural systems, however, resources fluctuate in abundance and diversity. These fluctuations may induce two independent effects: (1) changes in niche breadth and overlap, and (2) changes in population size as individuals and species migrate in or out of the community in response to resource availability. Correlations between these two effects may thus be incidental and need not imply a causal relationship.

**Results.**—I calculated correlations between niche breadth or niche overlap of each core species and its own effective population or the effective populations of competitors. All significant values appeared to be incidental results of each parameter's independent responses to changes in the resource base. For instance, *Chlorostilbon* niche breadth and electivity of low-density resources correlated negatively with *Colibri* effective population size ( $r = -.8057$ ,  $p < .01$  and  $r = -.8329$ ,  $p < .001$ , respectively), suggesting that competition from expanding *Colibri* populations forced a contraction of the *Chlorostilbon* niche. Abundant *Lobelia* flowers, however, often prompted both a high *Colibri* population and a narrow *Chlorostilbon* niche (cf. Figs. 12, 14). *Colibri* gross niche overlap correlated highly with the summed effective populations of all other species ( $r = .7791$ ,  $p < .01$ ). Both parameters, however, increased independently with increasing numbers of flowers. *Chlorostilbon* gross and adjusted niche overlaps correlated highly with *Chlorostilbon* effective population size ( $r = .7136$ ,  $p < .01$  and  $r = .8171$ ,  $p < .001$ , respectively), suggesting that intraspecific pressures within an expanding *Chlorostilbon* popu-

lation forced the increased overlap. *Chlorostilbon*'s influx into fields of high-density *Lobelia* flowers and its high overlap therein with other species, however, were independent events. Neither niche breadth nor electivity (of summed low-density resources) of any core species showed a significant response to its population size.

### CONCLUSIONS

It appears that the overall patterns of hummingbird foraging derive ultimately from individual responses to food availability. A given bird tends to visit those flowers or clumps it can exploit most efficiently and tends to bypass not only those flowers it cannot exploit so efficiently but also those flowers that other birds tend to visit. If the dispersion of nectar is such that the individual cannot efficiently obtain supplies that are neglected by others, the bird migrates to another habitat patch. The efficiency with which birds exploit particular flowers is primarily a species-specific phenomenon (see Wolf et al. 1972, 1976; Hainsworth 1973; Feinsinger and Chaplin 1975), as is their belligerence (see Wolf 1970, Stiles and Wolf 1970, Colwell 1973, Linhart 1973). Thus, the individual responses sum to a diversity of species-specific foraging patterns overlapping little over time, organized around the parameters of flower density: the density of a given clump determines which strategies are profitable, and the overall abundance and dispersion of flowers determines how many different patterns are profitable.

By virtue of their belligerence, the territorial *Amazilia saucerottei* individuals forced other birds to bypass most rich food sources. Thus *Amazilia* modified all other species' foraging patterns and served as the "organizer species" of the guild (*sensu* Price 1971, Root 1973). Although *Lampornis calolaema* and (to a lesser extent) *Amazilia tzacatl* dominated *Amazilia saucerottei*, these species preferred other habitats and scarcely affected guild organization in the study habitats. By virtue of their skill at traplining, *Chlorostilbon canivetii* individuals forced other birds to bypass many dispersed food sources. Thus *Chlorostilbon* in effect organized the foraging patterns of other nonterritorial species. The poor fit of the guild dominance-diversity curve to that predicted by the MacArthur broken-stick model (Fig. 13), which may yet have some relevance to bird groups organized through territoriality (Whittaker 1970; *personal communication*), resulted from *Amazilia saucerottei*'s monopoly on most choice segments of all resource dimensions and *Chlorostilbon*'s ability to trapline much of what remained.

Thus, foraging patterns of no species but *Amazilia* could respond to gross changes in the resource base. *Chlorostilbon*'s resources, aside from the forb *Lobelia laxiflora*, were fixed at a consistent level by *Amazilia*.

Other species responded only to those particular resource states that they could exploit efficiently and that *Amazilia* and *Chlorostilbon* could not or did not effectively use up. In particular, *Lobelia* provided superabundant nectar, and *Inga brenesii* provided opportunities for spatial and diurnal differentiation. *Philodice bryantae*, which tended to forage high, could consistently exploit the *Inga* nectar that *Amazilia* failed to exhaust, but responded less consistently to *Lobelia*. *Hylocharis eliciae* responded dramatically to *Lobelia*, which it could presumably exploit more efficiently than *Inga*. *Colibri thalassinus*, which could not defend rich resources as effectively as *Amazilia* and could not out-exploit *Chlorostilbon* at dispersed flowers, subsisted on nectar neglected by one or the other but, like other species, left the community when such supplies were no longer consistently available. *Heliomaster constantii* was restricted to the otherwise neglected *Mandevilla veraguensis* flowers. Although these and other peripheral species such as *Eupherusa eximia* showed no regular response to overall resource levels, they filled in most potential gaps between the principals' foraging patterns and the available nectar. Few potential resources were neglected by the guild as a whole; only at *Lobelia* did foraging patterns evolved for more discrete resources leave much nectar unused. The guild exploitation pattern was not only more predictable (cf. Tables 11, 13) but also less variable than patterns of individual species. Although MacArthur (1969b) states that species packing does not strictly apply when aggression is present, species packing theories do predict this close match between resource productivity and the aggregate utilization pattern (MacArthur 1970, 1972).

The buffering effect depended upon the ease with which species other than the principals could immigrate and emigrate. Between-patch migration is evidently a common strategy in tropical regions with patchy resource regimes. Root and Chaplin (1976) found that different milkweed patches in Colombian fields develop out of phase such that milkweed bugs can continuously exploit particular plant structures by migrating from patch to patch. Mountainous Central America possesses a great diversity of resource regimes (see Tosi 1969, Frankie et al. 1974, Heithaus 1974) and many birds, especially hummingbirds, migrate seasonally between these habitats (see Wagner 1946, Slud 1964, Skutch 1967, Wolf 1969, Colwell 1973, Wolf et al. 1976). Conversely, in regions where between-patch migration is limited, avian diversity may also be limited. Willis (1974) ascribes decreasing diversity in the Barro Colorado Island avifauna to the water barrier, which inhibits between-patch migration. Each small, homogeneous Caribbean Island supports only two hummingbird species, one large, one small (Lack 1973), possibly

a territorial specialist and a traplining generalist. Presumably, to exploit seasonal resource flushes peripheral species would have to migrate between islands or between island and mainland, and the cost of such migration must outweigh the benefits. Similarly, had all 14 species attempted to remain in the Monteverde study habitats year-around, each but *Amazilia* and *Chlorostilbon* would have faced times when all resources were controlled by dominant or more efficient species.

Habitats in the Monteverde region were remarkably heterogeneous, however. Neotropical species in general may be packed tightly along habitat gradients (cf. Janzen 1967b; MacArthur 1969a, 1972), and the Monteverde hummingbirds were no exception: each habitat possessed a different set of principal species. Thus individuals of these species could easily migrate to other habitats when the principals in those habitats failed to utilize all resource states. *Campylopterus hemileucurus* and *Eupherusa*, which frequently appeared in the study habitats, apparently organized the guild in the adjacent forest. Communities at lower elevations provided the study habitats with *Heliomaster* and *Hylocharis* individuals. The mesic forests and openings a few hundred meters distant donated two of their principals, *Lampornis* and *Elvira cupreiceps*. Even *Amazilia* and *Chlorostilbon* individuals apparently migrated between the study habitats and lowland communities. In addition, some species that appeared in the study habitats evidently make a profession of exploiting resource flushes in different habitats, employing a "fugitive species" strategy (*sensu* Hutchinson 1951). *Archilochus colubris* follows a peripheral, opportunistic pattern not only in Monteverde but also in the nucleus of its winter range (Wolf 1970). *Colibri thalassinus* appears to be an excellent migrator but a generalist in foraging strategy and habitat; *C. delphinae* may be even more opportunistic and less well integrated into particular communities. While *Philodice* is a foraging specialist and not strictly a fugitive species, its behavior suggests that it is subordinate to most other hummingbirds and habitually relies upon its unbirdlike *gestalt* to secure food. This pattern of opportunistic generalists and unique specialists, superimposed on a mosaic of organizer species which act as peripherals in neighboring communities, resembles the integration of insect-plant associations within a single habitat (Hutchinson 1965, Root 1973).

It is surprising that so many species whose potential foraging patterns, or virtual niches, overlap so extensively can coexist even temporarily. Yet if their spatial and temporal foraging patterns, efficiencies, and preferred habitats, i.e., their ecotopes, diverge at all, such species can always locate resources, if not in a particular community then in

another. As predicted by Klopfer and MacArthur (1961), MacArthur and Levins (1967), and May and MacArthur (1972), in such a regionally stable situation virtual niche overlap can be high without resulting in eventual extinction. The very lack of specialized feeding apparatus and specialized flowers in this successional situation allowed individuals, and the guild as a whole, to respond plastically to available nectar—the two species with highly modified beaks (*Heliomaster* and *Campylopterus*) played only minor roles.

In communities stable over evolutionary time, selection should nevertheless act to reduce this overlap between virtual niches by extinguishing those portions of each population's virtual niche with which other populations constantly interfere. The mature forests at Monteverde contain a diversity of distinctly shaped flowers exploited by hummingbirds with disparate beak shapes. In such communities, organization is based less on interference, more on co-evolution between particular flowers and particular birds (see Snow and Snow 1972, Stiles 1975). Less stable communities such as the secondary transition-zone habitats, however, not only reveal more about the selective forces involved but are also more abundant in nature.

#### ACKNOWLEDGMENTS

I gratefully acknowledge the untiring aid of R. B. Root at all stages in the evolution of this paper. R. K. Colwell, R. H. Whittaker, L. L. Wolf, and fellow graduate students of the Comparative Ecology Guild at Cornell also provided many helpful suggestions on the manuscript. The people of Monteverde graciously allowed study areas on their land and, along with my wife Claudia, provided considerable moral support. I thank W. H. and R. E. Buskirk, R. K. Colwell, W. C. Dilger, D. A. Lancaster, P. A. Opler, G. V. N. Powell, and F. G. Stiles for advice and encouragement during the fieldwork. Personnel of the Organization for Tropical Studies, especially L. Echeverría, helped with logistics. W. C. Burger of the Field Museum, L. Diego-Gómez of the Museo Nacional de Costa Rica, and L. Poveda of the Universidad de Costa Rica kindly identified plant specimens. Fieldwork was supported by an Andrew D. White Fellowship, a Cornell Graduate Fellowship, funds from an NSF training grant to the Section of Ecology and Systematics, and a grant from Mr. J. S. Dunning. The Department of Zoology, University of Florida, paid page charges.

#### LITERATURE CITED

- Ashmole, N. P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Syst. Zool.* **17**:292–304.
- Baker, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* **7**:37–41.
- Baker, M. C., and A. E. M. Baker. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. *Ecol. Monogr.* **43**: 193–212.
- Baldwin, S. P., H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds. Cleveland Museum Natural History, Cleveland, Ohio. 165 p.
- Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. *U.S. Natl. Mus. Bull.* **176**:1–506.
- Betts, M. M. 1955. The food of titmice in oak woodland. *J. Anim. Ecol.* **24**:282–323.
- Brian, M. V. 1956. Exploitation and interference in interspecies competition. *J. Anim. Ecol.* **25**:339–347.
- Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. *Ecology* **54**: 775–787.
- Brown, J. H., and G. A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* **54**:788–797.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* **76**:160–169.
- Caccamise, D. 1974. Competitive relationships of the common and lesser nighthawks. *Condor* **76**:1–20.
- Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proc. Natl. Acad. Sci. U.S.A.* **71**:3073–3077.
- Cody, M. L. 1974. Optimization in ecology. *Science* **183**:1156–1164.
- Colwell, R. K. 1973. Competition and coexistence in a simple tropical community. *Am. Nat.* **107**:737–760.
- Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. *Annu. Rev. Ecol. Syst.* **6**:281–310.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**:567–576.
- Colwell, R. K., B. J. Betts, P. Bunnell, F. L. Carpenter, and P. Feinsinger. 1974. Competition for the nectar of *Centropogon valerii* by the hummingbird *Colibri thalassinus* and the flower-piercer *Diglossa plumbea*, and its evolutionary implications. *Condor* **76**:447–452.
- Connell, J. H., and E. Orias. 1964. The ecological regulation of species diversity. *Am. Nat.* **98**:399–414.
- Culver, D. H. 1970. Analysis of simple cave communities: Niche separation and species packing. *Ecology* **51**:949–958.
- Emlen, J. M. 1966. The role of time and energy in food preference. *Am. Nat.* **100**:611–617.
- Enders, F. 1974. Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. *Ecology* **55**:317–328.
- Erlinge, S. 1972. Interspecific relations between otter *Lutra lutra* and mink *Mustela vison* in Sweden. *Oikos* **23**:327–335.
- Faegri, K., and L. van der Pijl. 1971. The principles of pollination ecology, 2nd ed. Pergamon, London. 291 p.
- Feinsinger, P. 1974. Organization of a tropical guild of nectarivorous birds. Ph.D. thesis. Cornell Univ., Ithaca, New York. 163 p.
- . 1976. Notes on the hummingbirds of Monteverde, Cordillera de Tilarán, Costa Rica. *Wilson Bull.* **87**: (in press).
- Feinsinger, P., and S. B. Chaplin. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. *Am. Nat.* **109**:217–224.
- Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical lowland wet and dry forest sites of Costa Rica. *J. Ecol.* **62**:881–919.
- Hainsworth, F. R. 1973. On the tongue of a hummingbird: Its role in the rate and energetics of feeding. *Comp. Biochem. Physiol. A. Comp. Physiol.* **46**:65–78.
- Hamilton, T. H. 1962. Species relationships and adap-

- tations for sympatry in the avian genus *Vireo*. *Condor* **64**:40–68.
- Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. *J. Anim. Ecol.* **22**:261–288.
- Heithaus, E. R. 1974. The role of plant-pollinator interactions in determining community structure. *Ann. Mo. Bot. Gard.* **61**:675–691.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* **54**:427–432.
- Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica. 206 p.
- Holdridge, L. R., W. O. Grenke, W. H. Hathaway, T. Liang, and J. A. Tosi, Jr. 1971. Forest environments in tropical life zones: A pilot study. Pergamon Press, New York. 747 p.
- Holmes, R. T., and F. A. Pitelka. 1968. Food overlap among coexisting sandpipers on northern Alaska tundra. *Syst. Zool.* **17**:305–318.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* **32**:571–577.
- . 1958. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**:415–427.
- . 1965. The ecological theater and the evolutionary play. Yale Univ. Press, New Haven, Connecticut. 139 p.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Connecticut. 302 p.
- Jaeger, R. G. 1974. Competitive exclusion: Comments on survival and extinction of species. *BioScience* **24**: 33–39.
- Janzen, D. H. 1967a. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* **21**:620–637.
- . 1967b. Why mountain passes are higher in the tropics. *Am. Nat.* **101**:233–249.
- . 1971. Euglossine bees as long distance pollinators of tropical plants. *Science* **171**:203–205.
- Klopfen, P. H., and R. H. MacArthur. 1961. On the causes of tropical species diversity: Niche overlap. *Am. Nat.* **95**:223–226.
- Lack, D. 1946. Competition for food by birds of prey. *J. Anim. Ecol.* **15**:123–129.
- . 1973. The numbers of species of hummingbirds in the West Indies. *Evolution* **27**:326–337.
- Legg, K., and F. A. Pitelka. 1956. Ecological overlap of Allen and Anna hummingbirds nesting at Santa Cruz, California. *Condor* **58**:393–405.
- Levins, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, New Jersey. 120 p.
- Linhart, Y. B. 1973. Ecological and behavioral determinants of pollen dispersal in hummingbird-pollinated *Heliconia*. *Am. Nat.* **107**:511–523.
- Linsley, E. G., J. W. MacSwain, and P. H. Raven. 1963. Comparative behavior of bees and Onagraceae, I, II. *Univ. Calif. Publ. Entomol.* **33**:1–58.
- Lyon, D. L. 1973. Territorial and feeding activity of broad-tailed hummingbirds (*Selasphorus platycercus*) in *Iris missouriensis*. *Condor* **75**:346–349.
- MacArthur, R. H. 1958. Population ecology of some warblers of northern coniferous forests. *Ecology* **39**: 599–619.
- . 1968. The theory of the niche. In R. C. Lewontin [ed.] *Population biology and evolution*. Syracuse Univ. Press, Syracuse, New York. 205 p.
- . 1969a. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* **1**:19–30.
- . 1969b. Species packing, and what interspecies competition minimizes. *Proc. Natl. Acad. Sci. U.S.A.* **64**:1369–1371.
- . 1970. Species packing and competitive equilibrium for many species. *Theor. Pop. Biol.* **1**:1–11.
- . 1972. *Geographical ecology: Patterns in the distribution of species*. Harper & Row, New York. 269 p.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proc. Natl. Acad. Sci. U.S.A.* **51**:1207–1210.
- MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**:377–385.
- MacArthur, R. H., and E. C. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* **100**: 603–609.
- McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. *Science* **167**:131–139.
- May, R. M. 1975. Some notes on estimating the competition matrix,  $\alpha$ . *Ecology* **56**:737–741.
- May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proc. Natl. Acad. Sci. U.S.A.* **69**:1109–1113.
- Miller, R. S. 1967. Pattern and process in competition. *Adv. Ecol. Res.* **4**:1–74.
- Morse, D. H. 1967. Foraging relationships of brown-headed nuthatches and pine warblers. *Ecology* **48**: 94–103.
- . 1974. Niche breadth as a function of social dominance. *Am. Nat.* **108**:818–830.
- Murray, B. G. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* **52**: 414–423.
- Nicholson, A. J. 1948. Competition for food among *Lucilia cuprina* larvae. *Int. Congr. Entomol. Proc.* **8**:277–281.
- Nilsson, N.-A. 1960. Seasonal fluctuations in the food segregation of trout, char, and whitefish in 14 North-Swedish lakes. *Rep. Inst. Freshwater Res. Drottningholm* **41**:185–205.
- Oertel, E. 1946. Effect of temperature and relative humidity on sugar concentration of nectar. *J. Econ. Entomol.* **39**:513–515.
- Orians, G. H., and M. F. Willson. 1964. Interspecific territories of birds. *Ecology* **45**:736–745.
- Ortiz-Crespo, F. I. 1972. A new method to separate immature and adult hummingbirds. *Auk* **89**:851–857.
- Park, T. 1962. Beetles, competition, and populations. *Science* **138**:1369–1375.
- Patrick, R. 1968. The structure of diatom communities in similar ecological conditions. *Am. Nat.* **102**: 173–184.
- Patrick, R., M. Hohn, and J. Wallace. 1954. A new method of determining the pattern of the diatom flora. *Not. Nat. (Phila.)* **259**.
- Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. *Ecology* **48**:333–351.
- . 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* **50**:1012–1030.
- . 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**:53–74.
- Pitelka, F. A. 1942. Territoriality and related problems in North American hummingbirds. *Condor* **44**: 189–204.
- . 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. *Ecology* **32**:641–661.

- Price, P. W. 1971. Niche breadth and dominance of parasitic insects sharing the same host species. *Ecology* **52**:587-596.
- Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. *Ecology* **47**:393-407.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* **37**:317-350.
- . 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* **43**:95-124.
- Root, R. B., and S. J. Chaplin. 1976. The life styles of tropical milkweed bugs, *Oncopeltus* (Hemiptera: Lygaeidae), utilizing the same hosts. *Ecology* **57**:132-140.
- Roughgarden, J. 1974. Niche width: Biogeographic patterns among *Anolis* lizard populations. *Am. Nat.* **108**:429-442.
- Sawyer, J. O., and A. A. Lindsey. 1971. Vegetation of the life zones in Costa Rica. *Indiana Acad. Sci. Monogr.* **2**:1-214.
- Schlising, R. A. 1970. Sequence and timing of bee foraging in flowers of *Ipomoea* and *Aniseia* (Convolvulaceae). *Ecology* **51**:1061-1067.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**:369-404.
- . 1974a. Resource partitioning in ecological communities. *Science* **185**:27-39.
- . 1974b. Some methods for calculating competition coefficients from resource utilization spectra. *Am. Nat.* **108**:332-340.
- . 1974c. The compression hypothesis and temporal resource partitioning. *Proc. Natl. Acad. Sci. U.S.A.* **71**:4169-4172.
- Schroder, G. D., and M. L. Rosenzweig. 1975. Perturbation analysis of competition and overlap in habitat utilization between *Dipodomys ordii* and *Dipodomys merriami*. *Oecologia* **19**:9-28.
- Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* **68**:113-151.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 212 p.
- Skutch, A. F. 1967. Life histories of Central American highland birds. *Publ. Nuttall Ornithol. Club* **7**:1-213.
- Slud, P. 1964. The birds of Costa Rica. *Bull. Am. Mus. Nat. Hist.* **128**:1-430.
- Snow, B. K., and D. W. Snow. 1972. Feeding niches of hummingbirds in a Trinidad valley. *J. Anim. Ecol.* **41**:471-485.
- Stiles, F. G. 1973. Food supply and the annual cycle of the Anna hummingbird. *Univ. Calif. Publ. Zool.* **97**:1-109.
- . 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**:285-301.
- Stiles, F. G., and L. L. Wolf. 1970. Hummingbird territoriality at a tropical flowering tree. *Auk* **87**:467-491.
- . 1973. Techniques for color-marking hummingbirds. *Condor* **75**:244-245.
- Svärdson, G. 1949. Competition and habitat selection in birds. *Oikos* **1**:157-174.
- Tosi, J. A., Jr. 1969. Mapa ecológico de Costa Rica. Centro Científico Tropical (Tropical Science Center), San José, Costa Rica.
- Vandermeer, J. H. 1972. Niche theory. *Annu. Rev. Ecol. Syst.* **3**:107-132.
- Wagner, H. O. 1945. Notes on the life history of the Mexican violet-ear. *Wilson Bull.* **57**:165-187.
- . 1946. Food and feeding habits of Mexican hummingbirds. *Wilson Bull.* **58**:69-93.
- Ward, P. 1965. Feeding ecology of the black-faced dioch *Quelea quelea* in Nigeria. *Ibis* **107**:173-214.
- Whittaker, R. H. 1970. Communities and ecosystems. Macmillan, New York. 162 p.
- Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. Niche, habitat, and ecotope. *Am. Nat.* **107**:321-338.
- Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* **44**:153-169.
- Willson, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. *Condor* **72**:169-174.
- Wolf, L. L. 1969. Female territoriality in a tropical hummingbird. *Auk* **86**:490-504.
- . 1970. The impact of seasonal flowering on the biology of some tropical hummingbirds. *Condor* **72**:1-14.
- Wolf, L. L., F. R. Hainsworth, and F. G. Stiles. 1972. Energetics of foraging: Rate and efficiency of nectar extraction by hummingbirds. *Science* **176**:1351-1352.
- . 1976. Ecological organization of a tropical, highland hummingbird community. *J. Anim. Ecol.* **45**: (in press).
- Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. *Ecology* **52**:336-342.