ECOLOGY, FLOWERING PHENOLOGY, AND HUMMINGBIRD POLLINATION OF SOME COSTA RICAN *HELICONIA* SPECIES[1]

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Abstract. Nine hummingbird-pollinated species of *Heliconia* occur together at Finca La Selva, in the wet Caribbean lowlands of Costa Rica. In forest habitats, *Heliconia* clumps (clones) are typically small; in more open areas, many clumps attain large size. This probably reflects differences in light intensity and degree of vegetative competition in these habitats.

Nine species of hummingbirds regularly visit *Heliconia* flowers at La Selva. The four hermits are nonterritorial, traplining foragers with long, curved bills. Non-hermits frequently hold territories at *Heliconia* clumps, and have short, straight bills. Pollination by hermits tends to produce more cross-pollination; territorial hummingbirds increase self-pollination. Different *Heliconia* species appear to be specialized for pollination by either hermits or non-hermits, largely through components of the caloric phenotype: amount and timing of nectar production, rate of inflorescence and flower production, and morphological parameters that affect the energetic efficiency of nectar-harvesting hummingbirds. Habitat may influence pollination systems through its effects on clump size and thus on the number of flowers a clump can have at any one time. Ultimately, specialization for hermits or non-hermits may depend on the degree of self-compatibility of the different *Heliconia* species.

Hermit-pollinated *Heliconia* mostly show sequential and nonoverlapping flowering peaks, probably resulting from competition for pollinators and/or selection against hybridization. Two hermit-pollinated species bloom simultaneously, thereby inducing the birds to utilize an otherwise little-used microhabitat. *Helicona* species pollinated by non-hermits bloom in the early to middle rainy season, and are mostly separated by habitat.

Isolating mechanisms among sympatric *Heliconia* species involve both spatial and temporal patterns of partitioning available pollinators. Floral parameters include mechanical (different site of pollen deposition on the bird) and ethological (caloric and visual factors affecting flower choice) mechanisms. Selection for pollinator specificity may result in convergence of blooming peaks, provided that other isolating mechanisms are present. Human activity has broken down some habitat barriers by producing large areas of second growth.

Key words: Community interactions; competition; Heliconia; hummingbirds; phenology; pollination; resource partitioning; tropical rainforest; tropical seasonality.

INTRODUCTION

When sympatric plant species flower simultaneously, they may have to compete for pollinators. Levin and Anderson (1970) argued that under such circumstances, if the plants differ only in relative abundance, there will be strong selection against the rarer species, leading to its elimination from the community or to its divergence from the more abundant species in some aspect of floral phenology. In fact, it is probably very unusual to find in nature simultaneously flowering species that are identical in floral phenology; an array of species differing in various parameters seems more likely. If these species are also closely related taxonomically, not only competition for pollinators but also means of reducing hybridization and promoting pollinator specificity must be considered. This paper deals with an array of sympatric plant species in the genus

Heliconia L. (Musaceae) that share a common group of pollinators, the hummingbirds. In particular, I shall focus on what Heinrich and Raven (1972) have called the "caloric phenotype" of the plants: the amount and concentration of nectar secreted, the morphological parameters that affect harvesting of this nectar by the birds, and the ecological factors influencing the rate and timing of flowering.

The "platanillos" or "wild plantains" of the genus *Heliconia* are moderate-to-large-sized herbs (Table 1) with banana-like leaves. They propagate vegetatively by rhizomes, and some species readily form large clones or "clumps." In its 2nd yr or later, each individual plant in a clump produces an inflorescence composed of several to many showy bracts, each of which encloses several flowers. This inflorescence opens, bract by bract, over a period of days or weeks; flowering usually starts in the older bracts before the inflorescence has fully opened. In all species examined so far, each flower lasts only 1 day. The flowers are tubular, of varying length and curvature (Fig. 1). Further discussion of the morphology of
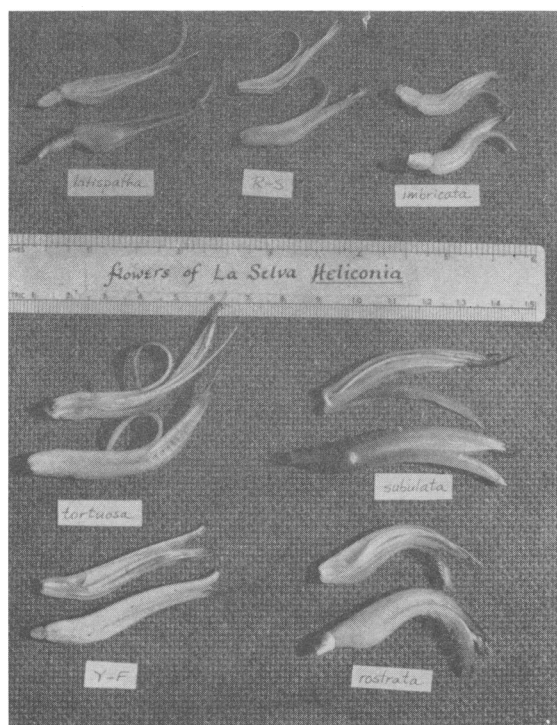
FIG. 1. Flowers of seven species of La Selva *Heliconia*. Name changes in this paper are as follows: "*rostrata*" = *pogonantha*, "*subulata*" = H-3, "Y-F" = H-16, "R-S" = H-17, "*tortuosa*" = H-18.

(Daniels and Stiles, *unpubl. data*). (The species called "*acuminata*" by Linhart (1973) is referred to here as H-3; Linhart's "*tortuosa*" is here called H-18. The proper name for the species called "*rostrata*" by Wolf et al. (1972) is *pogonantha*).

STUDY AREA

This study was done at Finca La Selva, in the Sarapiquí lowlands of northeastern Costa Rica. The topography, climate, and flora of La Selva have been described by Holdridge et al. (1971), and the avifauna has been studied by Slud (1960). I completed most of my research between February 1971 and October 1972, but have also made observations during August and September 1968, July and August 1969, and March, April, and July 1970. Monthly temperature and rainfall for the months of this study, as well as longterm averages (1963–71) are given in Fig. 2.

The major part of La Selva is covered by virgin forest. However, most *Heliconia* species cannot tolerate deep shade, and are found only at breaks in the forest canopy. The smallest and most ephemeral light gaps result from tree falls, are seldom over 20–30 m in diameter, and are usually closed (at least to *Heliconia*) within a very few years by rapid growth of woody plants. Somewhat larger and more permanent light gaps may occur along forest streams, and at numerous small, open swamps that form in poorly drained pockets where there is standing water all year. The largest and most permanent natural light gaps in tropical forest occur along the larger streams and rivers, where periodic inundations and unstable substrates may keep extensive areas free of trees.

Manmade breaks in the forest canopy are frequently larger and more permanent than natural ones and can greatly increase the available second-growth and forest-edge habitat, thereby altering drastically the distribution and abundance of some *Heliconia*. At La Selva fairly extensive tracts of second growth

Heliconia inflorescences and flowers is given by Smith (1966).

The genus *Heliconia* is represented in Costa Rica by some 35 species, distributed mainly in the humid life zones of lower and middle altitudes (Stiles, *unpubl. data*). Unfortunately, the taxonomy and nomenclature of *Heliconia* are currently in a chaotic state, and I am unable to assign definite names to several of the taxa discussed here. Rather than complicate matters further, I shall refer to these species by taxon numbers, as used in a revision of the genus in Costa Rica currently in progress

TABLE 1. Gross morphology and coloration of plants and inflorescences of La Selva *Heliconia*

Species	Plant height (m)	Aspect of inflorescence	Length of inflorescence (rachis) in cm	Color of branch bracts	Color of flowers
H. wagneriana	2½–4	erect	40–60	red, bordered with white and green	green
H. imbricata	3–6	erect	30–60	red	pale green
H. latispatha	2–5	erect	35–60	orange or red and yellow	green or yellow and green
H. mariae	6–10	pendant	45–85	red	pink
H. pogonantha	4–8	pendant	60–150	red and yellow	yellow
H-17	1½–4	erect	25–60	red, with yellow rachis	yellow
H-3	2–5	erect	6–12	red	yellow with red-orange base
H-18	½–2½	erect	20–30	red	yellow
H-16	1–2½	erect	7–12	yellow	pale yellow
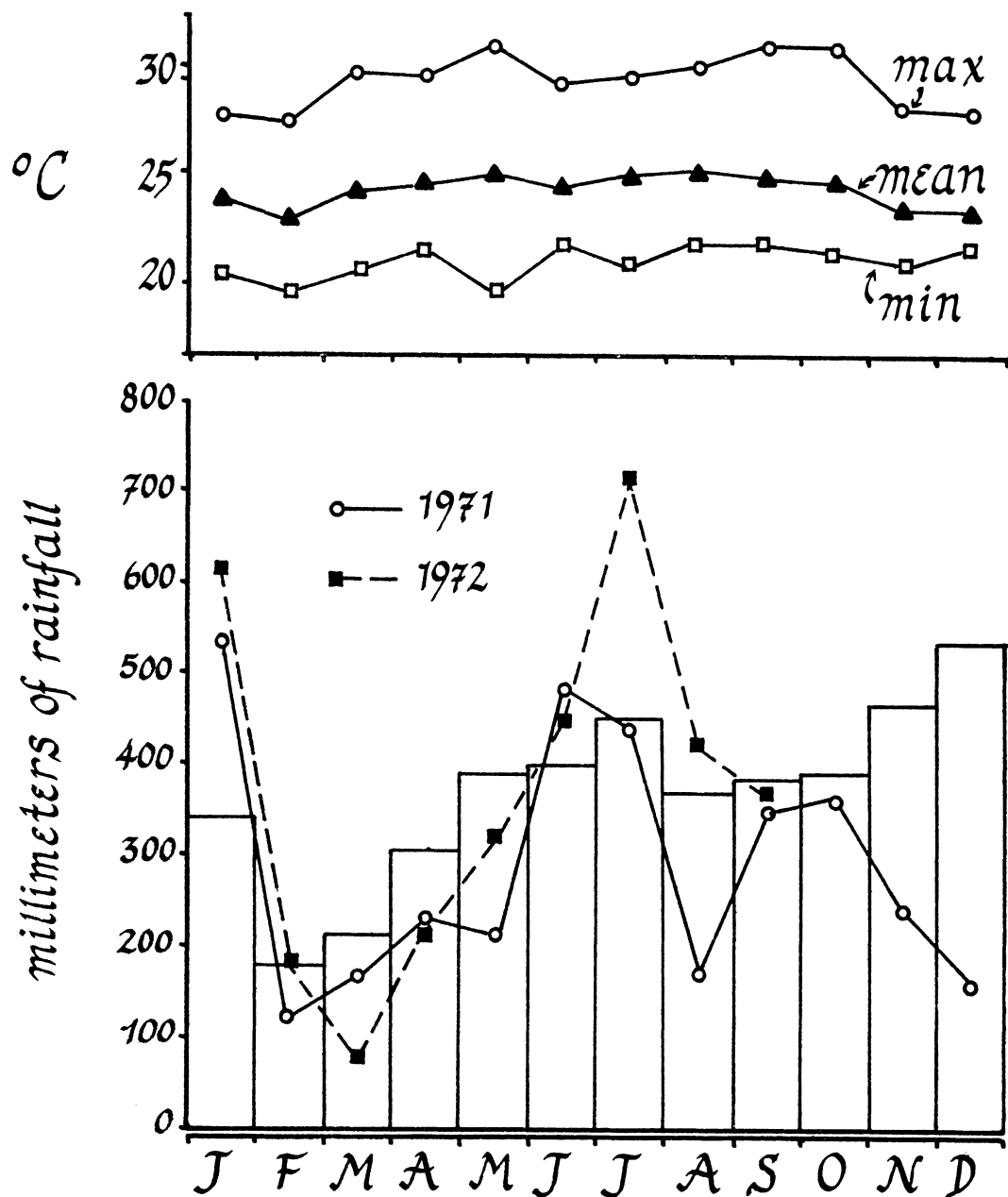
FIG. 2.   Monthly temperature and rainfall data for La Selva.   Upper graph: mean daily temperatures, October 1969–August 1971.   Lower graph: mean monthly rainfall for 1963–71 (bar graphs), and monthly rainfall during the period of this study.

of various ages occur in several areas. Since the time of Slud's (1960) study, the only major changes in the habitat at La Selva have probably been the abandonment of cacao and banana plantations and the invasion of these by second-growth plants, and the continued growth of areas that were previously in pasture or second growth. There has also been sufficient deforestation in the surrounding areas that La Selva is now a peninsula of forest projecting into

a sea of pastures and cultivated land. A large, continuous expanse of forest still exists to the south, towards the Cordillera Central.

METHODS AND MATERIALS

I assessed distribution and relative abundance of *Heliconia* in different habitats at La Selva by counting clumps of the various species along 10 census routes during March 1972. Clumps were classified

TABLE 2. Abundance of *Heliconia* clumps and plants along census routes at La Selva, March 1972

Census route	1	2	3	4	5	6	7	8	9	10
Approximate length (m)	2250	500	750	500	600	800	850	1850	1900	600
Habitat	forest	small forest stream	larger forest stream	open forest swamp	old second growth	old second growth	over grown cacao	shaded river-bank	open river-bank	young second growth
Species										
H. wagneriana										
No. clumps	0	0	0	0	23	1	12	11	15	24
No. plants	0	0	0	0	168	3	117	114	312	486
Plants/100 m	0	0	0	0	28.0	0.4	13.8	6.2	16.4	81.1
H. imbricata										
No. clumps	0	0	2	7	92	29	70	25	12	6
No. plants	0	0	6	39	1353	453	720	570	216	132
Plants/100 m	0	0	0.8	7.8	225.8	56.7	84.8	30.8	11.4	22.0
H. latispatha										
No. clumps	0	0	0	0	19	4	17	28	25	22
No. plants	0	0	0	0	211	21	207	434	694	502
Plants/100 m	0	0	0	0	35.2	2.6	24.4	23.5	36.5	88.7
H. mariae										
No. clumps	0	0	0	0	2	0	0	0	0	0
No. plants	0	0	0	0	60	0	0	0	0	0
Plants/100 m	0	0	0	0	10.0	0	0	0	0	0
H. pogonantha										
No. clumps	5	3	24	14	0	103	9	3	0	6
No. plants	24	18	207	96	0	1375	45	18	0	63
Plants/100 m	1.1	3.6	27.6	19.2	0	197.0	5.3	1.0	0	10.5
H-17										
No. clumps	12	45	13	7	0	0	0	0	0	0
No. plants	90	351	93	29	0	0	0	0	0	0
Plants/100 m	4.0	70.2	12.4	5.8	0	0	0	0	0	0
H-3										
No. clumps	5	12	40	66	5	5	6	11	4	0
No. plants	33	54	330	822	51	60	63	180	48	0
Plants/100 m	1.5	10.8	44.0	164.4	8.5	7.5	7.4	9.7	2.5	0
H-18										
No. clumps	41	29	15	4	2	14	0	0	0	0
No. plants	321	150	90	12	6	149	0	0	0	0
Plants/100 m	14.3	30.0	12.1	2.4	1.0	18.6	0	0	0	0
H-16										
No. clumps	20	2	1	0	0	2	0	0	0	0
No. plants	69	6	3	0	0	6	0	0	0	0
Plants/100 m	3.1	1.2	0.4	0	0	0.8	0	0	0	0
Total plants/100 m	24.0	115.8	97.3	199.6	308.5	283.6	135.7	71.2	66.8	202.3
Total no. of species	5	5	6	5	6	7	5	5	4	4

as small (1–5 plants), medium (6–20), large (20–50), or very large (50 plus). The census routes and habitats are listed in Table 2, in order of increasing openness. The routes were chosen because they provide a fairly representative selection of the habitats available for *Heliconia* and associated hummingbirds in the Sarapiquí region. Routes 8 and 9 were censused from a boat; all others were covered on foot.

The numbers of bracts per mature inflorescences and number of flowers produced per bract, were counted for all *Heliconia* species at La Selva. For the commoner species I made daily checks of several inflorescences to determine the rate and sequence of flower opening. For each species, total corolla length and effective corolla length (the approximate minimum distance between the entrance to the corolla tube and nectar chamber) were measured.

For a quantitative evaluation of blooming seasonality, I counted the number of inflorescences and fresh flowers on 10 census clumps of each *Heliconia* at approximately monthly intervals. (For the very uncommon *H. mariae* only two census clumps were used.) I classified the age and flowering status of

TABLE 3. Bill morphology, body weights, and preferred habitats of hummingbirds that regularly visit *Heliconia* flowers at La Selva

Hummingbird species	Body weight (g)[a]	Bill length (mm)[a, b]	Bill curvature	Preferred habitat
Hermits				
Eutoxeres aquila	10.5	36.7[c]	very strongly decurved	forest, forest edge, old second growth
Phaethornis superciliosus	6.0	40.8	moderately decurved	forest, forest edge, old second growth
Threnetes ruckeri	5.8	33.2	slightly decurved	forest, forest edge, old second growth
Glaucis hirsuta	5.4	33.0	''	young or old second growth, forest edge
Non-hermits				
Chalybura urochrysia	6.6	26.4	straight	forest, forest edge, old second growth
Thalurania furcata	4.3	23.5	''	forest, forest edge, old second growth
Amazilia tzacatl	5.3	24.8	''	young or old second growth
Amazilia amabilis	4.0	22.1	''	old second growth, forest edge
Florisuga mellivora	7.0	23.4	''	forest, forest edge, second growth

[a] Mean, $N = 10$; for sexually dimorphic species, 5 of each sex used.
[b] Length of total culmen (Stiles 1973).
[c] Measured along the arc of the culmen.

each inflorescence by a 7-stage system. The stages ranged from 0: inflorescence just appearing, no flowers, through 6: inflorescence old, dying or dead. In addition, a few inflorescences of most species were marked as they appeared, and were checked at shorter intervals to determine more precisely the duration of each age and flowering stage.

Since nectar is the resource in *Heliconia* flowers that is exploited by hummingbirds, nectar production was examined in some detail. Nectar was collected with fine calibrated capillary tubes (25, 50, or 100-μl Drummond "Microcaps"). In most *Heliconia*, the long and/or curved corolla tube prevented direct access to the nectar chamber by the capillary tube, and the flowers had to be picked and dissected to extract nectar. Flowers were bagged before they opened, either at dawn or on the preceding evening. Groups of 10 or more flowers were then sampled at regular intervals through the day; differences in mean nectar content could be used to estimate nectar production during each sample period.

I obtained nectar concentrations by measuring the refractive indices of the nectars with a temperature-compensated hand refractometer (National Instrument Co., Baltimore). Nectar of most flowers, including those of *Heliconia*, is essentially an aqueous solution of sucrose, fructose, and glucose in varying proportions (Percival 1961). These three sugars contain about an equal number of calories per gram. The 12-carbon sugar sucrose has a refractive index and a molecular weight twice those of the 6-carbon sugars glucose and fructose. Thus 1 mol of the former contains the same number of carbon atoms, yields about the same number of calories, and has the same refractive index as 2 mol of glucose or fructose. One can therefore express nectar concentrations in terms of an equivalent sucrose concentration, and calories per mol of nectar can be easily calculated. (1 μl of 1.0 molar sucrose = 1.35 cal). Given such details of flowering phenology as amount of nectar per flower, number of flowers per inflorescence or per clump, one can quickly calculate calories per flower, and can view spatial or seasonal blooming patterns on a caloric basis.

Data on hummingbird utilization of *Heliconia* were gathered on three censuses, commencing at 0600, 1000, and 1400 h during 1 day in April, August, and October 1971 and January 1972, for each of three routes. This combination of census routes and times of year allowed me to observe all the La Selva *Heliconia* in good bloom. In addition, I conducted two or three all-morning watches (usually 0500–1100 or 1130 h) at clumps of each species of *Heliconia*. During these observations I recorded each instance of foraging or territoriality at *Heliconia*, and the species of hummingbird involved. A hummingbird was considered to be territorial if it remained in the immediate vicinity of a clump (or several adjacent clumps) of *Heliconia* for at least 1 h and if during this time it fed at the clump and attempted to prevent other hummingbirds from doing so by threatening or attacking them (Wolf 1969, Stiles and Wolf 1970). Observations of hummingbirds feeding at *Heliconia* flowers were made through 10-power binoculars, and sites of pollen deposition on the bird were noted. Hummingbirds were also captured by mist-netting in or near feeding areas and examined for presence of *Heliconia* pollen on bills or plumage. Weights (to the nearest 0.1 g) and bill measurements (total culmen, to nearest 0.5 mm) were also taken on mist-netted birds (Table 3).

RESULTS

Ecology of the plants

Eight species of *Heliconia* occur commonly at La Selva. A ninth species, *H. mariae*, is known
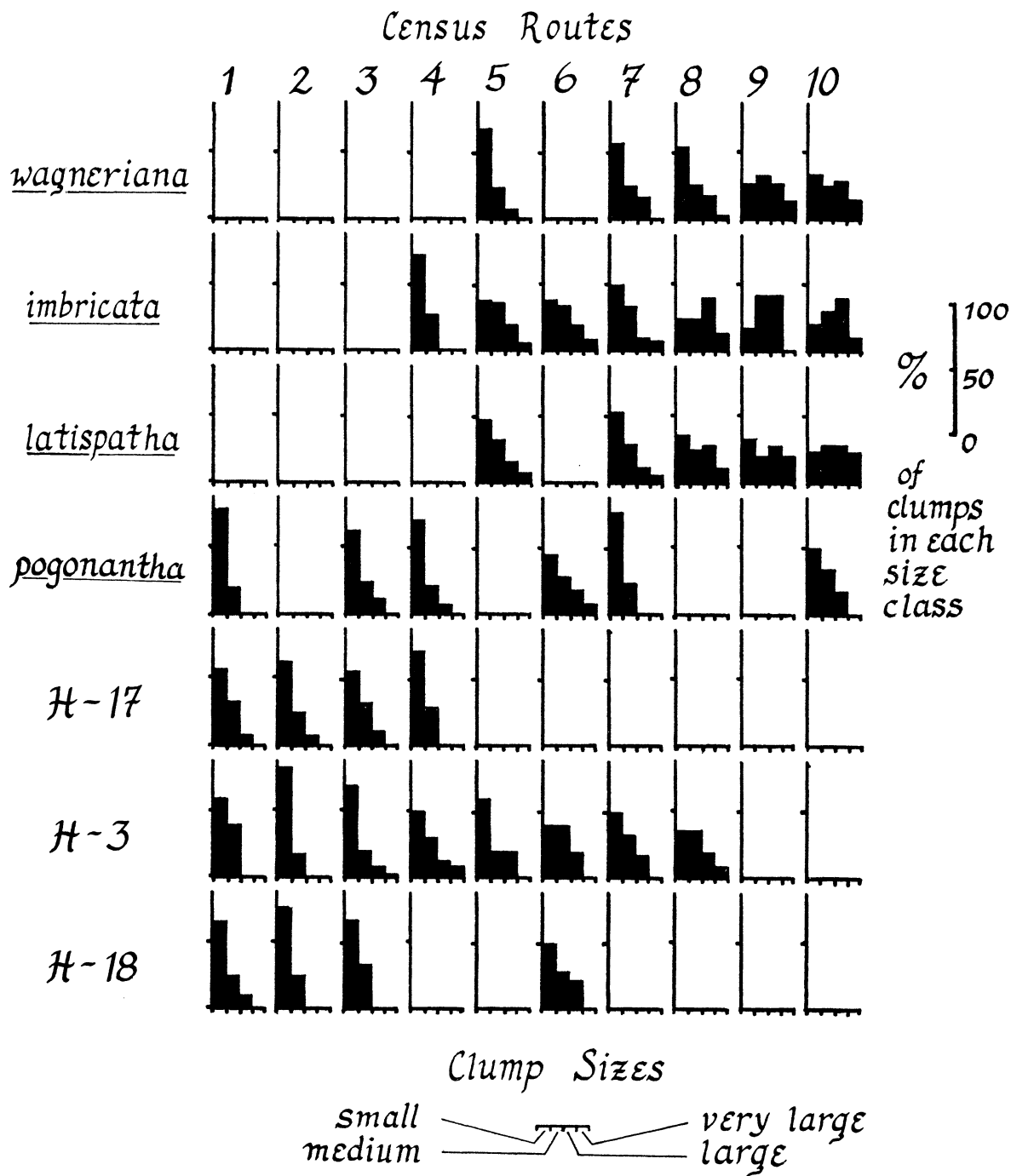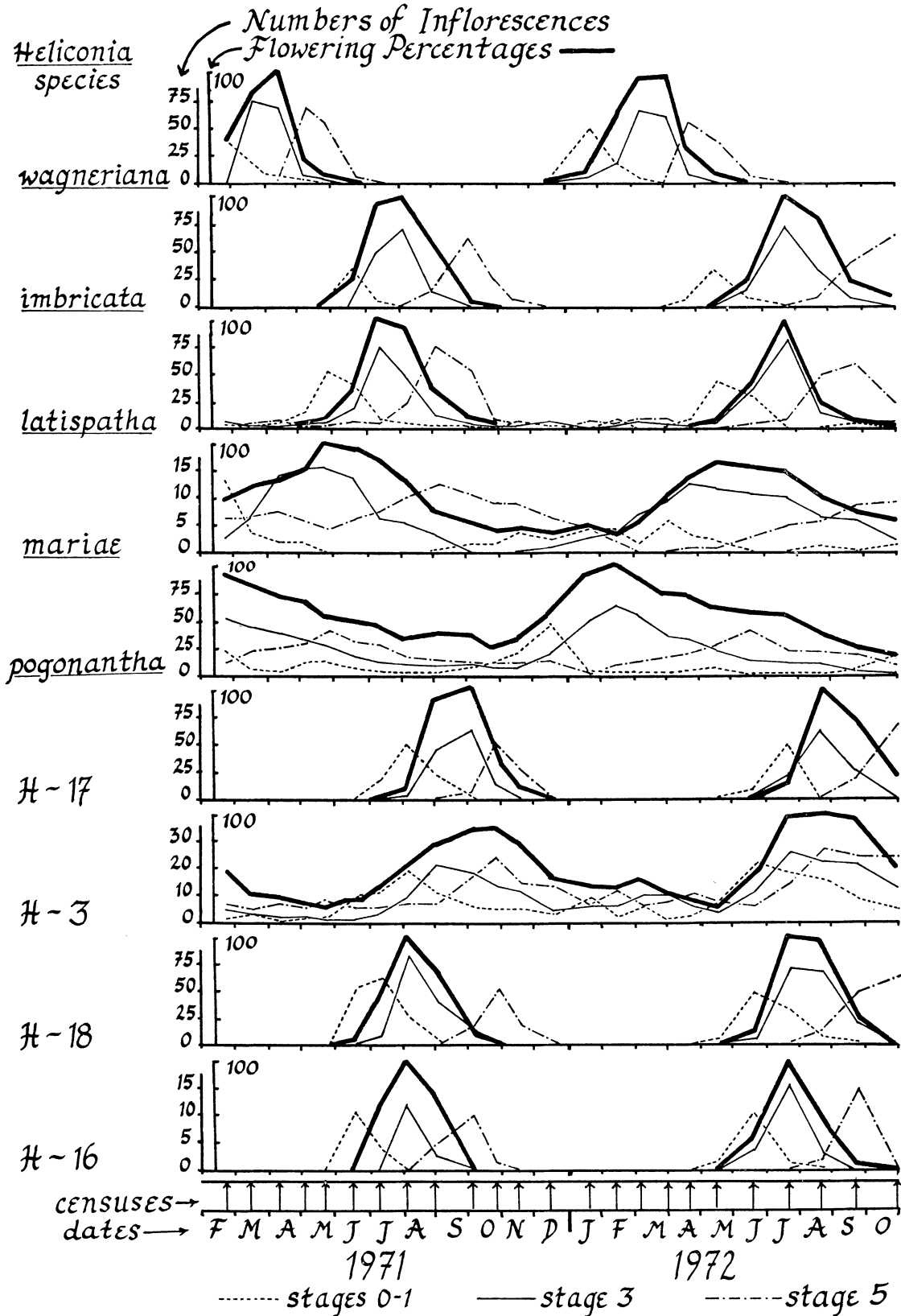
Census Routes

FIG. 3. Percentage distribution of *Heliconia* clumps in four size categories along census routes at La Selva. The size classes are: small, 1–5 plants; medium, 6–20 plants; large, 20–50 plants; very large, over 50 plants. Smaller clumps are preponderate in forested habitats, and larger clumps in more open habitats. Census routes arranged in order of increasing open habitats.

→

FIG. 4. Seasonality of inflorescence and flower production of La Selva *Heliconia* species. Flower counts expressed as % of maximum number of flowers recorded on 10 census clumps of each species (except only 2 clumps of *mariae*) during the given blooming season (or during the entire study period for continuously blooming species). In-florescence counts are numbers of young (sta. 0–1), profusely flowering (sta. 3), and mostly fruiting (sta. 5) in-florescences recorded on censuses.

Numbers of Inflorescences
Flowering Percentages ——

Heliconia species: *wagneriana*, *imbricata*, *latispatha*, *mariae*, *pogonantha*, H ~ 17, H ~ 3, H ~ 18, H ~ 16

censuses→
dates→ F M A M J J A S O N D J F M A M J J A S O
1971   1972

········ stages 0-1   —— stage 3   —·—·— stage 5

only from two large clumps on the Point. The morphological characteristics of the plants and inflorescences of these species are summarized in Table 1. As a group, *Heliconia* are least abundant in virgin forest and most abundant in second growth. Along forest streams and especially open swamps, *Heliconia* may be several times more abundant than inside the forest itself (Table 2). In these essentially natural habitats, the overall abundance of *Heliconia* appears to parallel relative size and permanence of the associated light gaps in the forest canopy. The highest densities of *Heliconia* occur in second growth. Old second growth (the East Boundary and the Point) supports the highest number of species, young open second growth (as at Puerto Viejo and along the Río Sarapiquí) the fewest.

Three groups of *Heliconia* species can be roughly distinguished at La Selva: highly shade-tolerant species found regularly within virgin forest; species requiring high light intensities and occurring only in the most open habitats; and species tolerating a wide range of light intensities and found in a variety of habitats. Light intensity is not the only environmental gradient important in *Heliconia* distribution: temperature, moisture, slope, and soil type are doubtless important, at least to some species (Sheffy, *unpubl. data*). However, none of these factors appears able to produce the relatively clearcut breakdown of species given by light intensity, at least among La Selva *Heliconia*.

The forest-based *Heliconia* at La Selva are H-16, H-17, and H-18. Of these, only H-18 is found to any extent in older second growth, where a canopy of small trees is fairly well developed. It is possible that at least H-18 could do well in full sunlight, but cannot stand the vegetative competition of other second-growth plants, especially the vines and shrubs of young second growth. Within the forest, H-17 and H-18 are usually found at small-to-moderate-sized light gaps. H-16 is a relatively uncommon species found scattered through the forest, often at no discernible light gap. As a group, forest *Heliconia* tend to occur in small clumps (Fig. 3), reflecting the relatively small, short-lived light gaps of these habitats: these *Heliconia* may not have enough time to attain large clump size before their light gap is closed.

True inhabitants of young, very open second growth are *H. wagneriana, H. latispatha,* and, perhaps to a lesser extent, *H. imbricata*. Only the last-named occurs in essentially forested country, and then only at the largest and most persistent of light gaps. The *Heliconia* of this group were, before widespread deforestation, probably restricted to open riverbanks or (*imbricata*) sunny forest streams and swamps. All of these species reproduce vegetatively very rapidly and within a short time will form large clumps. Indeed large clumps are if anything more common than small ones in young second growth (Fig. 4) probably because many of the small clumps are overwhelmed by vines and other second-growth plants; only large clumps can long persist under such conditions.

Heliconia pogonantha and H-3 appear to tolerate a wide range of light conditions and occur in a diverse array of habitats: moderate to fairly deep shade along forest streams, at moderate-sized light gaps in forest (as at the small swamps in poorly drained glens), second growth of various ages, and open swamps. *Heliconia mariae* probably belongs in this group also, since in other areas I have found it common in similarly diverse habitats.

Both within and between species clump size tends to be larger in more open habitats. In forest habitats, no more than 20% of the clumps of any species are large or very large, whereas in young open second growth 40% to 50% of the clumps of most species are large to very large (Fig. 3).

Flowering phenology

All *Heliconia* species at La Selva have a pronounced seasonal peak of flowering and production of inflorescences (Fig. 4). Species that bloom year-round are *pogonantha*, with a peak in the early dry season (cf. Fig. 2); *mariae*, with a peak in the late dry or early wet season; and H-3, with its peak in the middle to late rainy season. Although a few *latispatha* inflorescences could be found in virtually every month at La Selva, the species as a whole shows a sharply defined peak in the early rainy season. Species having short, entirely discrete blooming seasons are *wagneriana* in the dry season and *imbricata*, H-16, H-17, and H-18 in the rainy season. For the *Heliconia* community generally, the rainy season is the peak of flowering, when up to 8 species are blooming compared to at most 4 (or 5 including *latispatha*) in the dry season. The time lags between high counts of preflowering (stages 0–1), profusely flowering (stage 3), and mostly fruiting (stage 5) inflorescences appear to be fairly constant within species (Fig. 4). This permits an estimate of the average lifetime of an individual inflorescence of each species. Such estimates range from 2 to 3 months in H-3 and H-17 to 6 months or more in *pogonantha* and *mariae* (Table 4).

For most *Heliconia* a high rate of flower production (short interval between flowers per bract), a small number of fertile bracts per inflorescence, and a short inflorescence life seem to go together (Table 4) and to be correlated with a short, discrete blooming season (Fig. 4). A given inflorescence of most species produces some 100 to 300 flowers in a lifetime of 2–4 mo. Highest rates of flower production
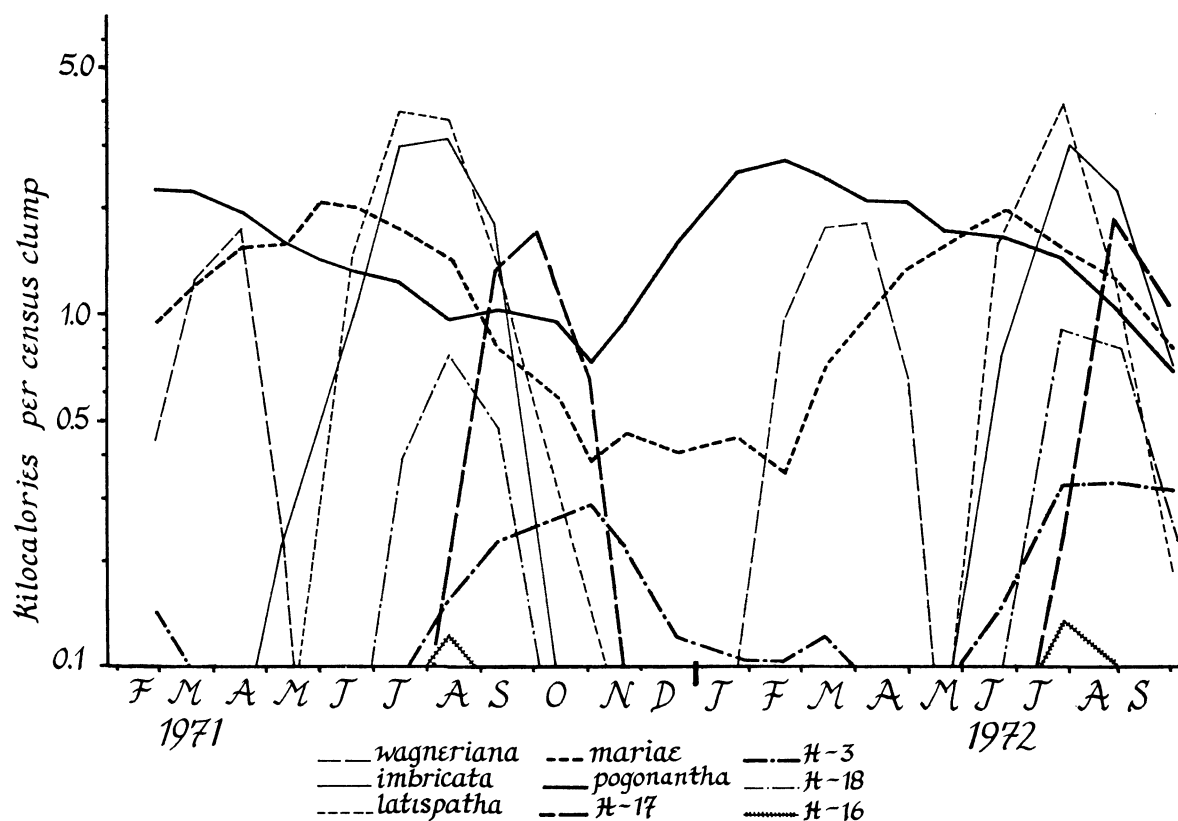
FIG. 5. Mean number of kcal available in flower nectar per census clump on monthly flower counts, as derived from the caloric equivalents per flower given in Table 5.

occur in *latispatha*, H-17, and *imbricata*. The larger number of bracts of *imbricata*, and the greater number of flowers per bract in *latispatha* and H-17, result in a fairly similar daily production of flowers per stage 3 inflorescence. Lower daily flower production per inflorescence is seen in H-3, H-16, and H-18 because of their smaller number of fertile bracts per inflorescence.

Heliconia mariae and *pogonantha* show a different pattern in several respects. These species combine a large number of bracts with low flowering rates and long inflorescence life. Their inflorescences are thus considerably more massive than those of other species; it seems likely that the pendant habit evolved in connection with the problem of supporting a large, heavy inflorescence. In these species, in-

TABLE 4. Inflorescence and flower production of La Selva *Heliconia*

Species	% of plants with inflorescences		No. fertile bracts per inflorescence[a]	No. flowers per fertile bract	Total no. flowers per inflorescence	No. days between flowers in a given bract[b]	Length of blooming period of inflorescence (mo)	No. flowers per stage 3 inflorescence[a]
	1971	1972						
H. wagneriana	59.8	58.4	13.2 (8–17)	ca. 20	ca. 250	2 (2–5)	ca. 3	3.3 (1–6)
H. imbricata	51.5	52.6	22.8 (18–32)	ca. 10	ca. 225	2 (1–5)	ca. 4	4.2 (2–8)
H. latispatha	48.8	53.7	14.3 (12–17)	ca. 20	ca. 275	2 (1–4)	3–4	5.0 (2–9)
H. mariae	43.4	38.5	59.5 (44–72)	ca. 15	ca. 900	6 (4–9)	6–7	4.3 (2–8)
H. pogonantha	43.2	44.7	34.6 (16–53)	ca. 20	ca. 750	5 (3–8)	5–7	3.3 (1–7)
H-17	36.9	49.8	12.2 (6–15)	15–20	ca. 200	2 (1–4)	ca. 3	1971: 1.7 (0–7)
								1972: 4.1 (1–8)
H-3	24.6	27.8	6.0 (4–9)	10–20	ca. 80	3 (2–5)	2–3	1.0 (0–3)
H-18	35.1	37.1	8.8 (7–10)	ca. 15	ca. 135	3 (2–6)	ca. 3	1.4 (0–3)
H-16	34.3	36.8	5.7 (3–7)	ca. 20	ca. 110	3 (2–5)	ca. 3	1.3 (0–3)

[a] Mean and range, $N = 10$.
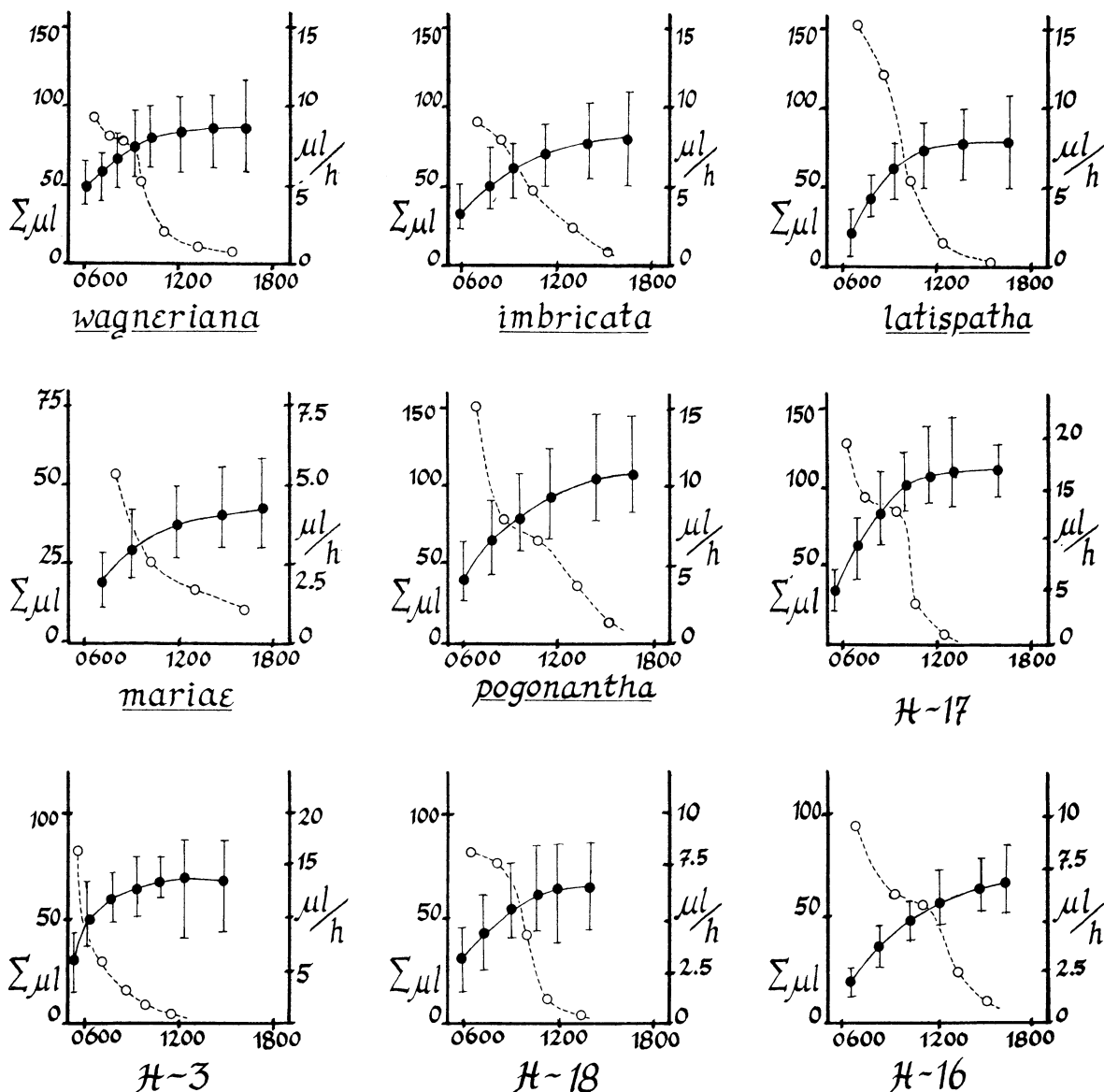[b] Mode and approximate range for a bract in the middle of the inflorescence.

Fig. 6. Daily pattern of nectar secretion of flowers of La Selva *Heliconia*. $\Sigma\mu$l = solid circles = total microliters of nectar in bagged flowers sampled at different times of day (mean and range); μl/h = open circles = average hourly rate of nectar production between samples.

florescences are mostly produced in a relatively short time; the long life of the inflorescence is largely responsible for the long blooming season. H-3, the other species that blooms year-round, relies on relatively continuous production of small, short-lived inflorescences.

The "percentage of plants with inflorescences" (Table 4) is that proportion of plants present at the start of a blooming season (or period of peak bloom for those species flowering year-round) which actually produced inflorescences during that season (or peak of blooming). Since the individual *Heliconia* plants usually flower in their 2nd yr, a given

clump will, during any one season, contain a high proportion of nonblooming plants. Unfortunately, I did not record age of plants during the censuses but only counted numbers of plants. The highest percentages of plants with inflorescences occurs in those species of open areas with short blooming seasons: *wagneriana, imbricata,* and *latispatha.* Lower percentages are observed in some forest species with short blooming seasons. Of those species blooming year-round, *pogonantha* and *mariae* have intermediate inflorescence-to-plant percentages, while that of H-3 is much lower.

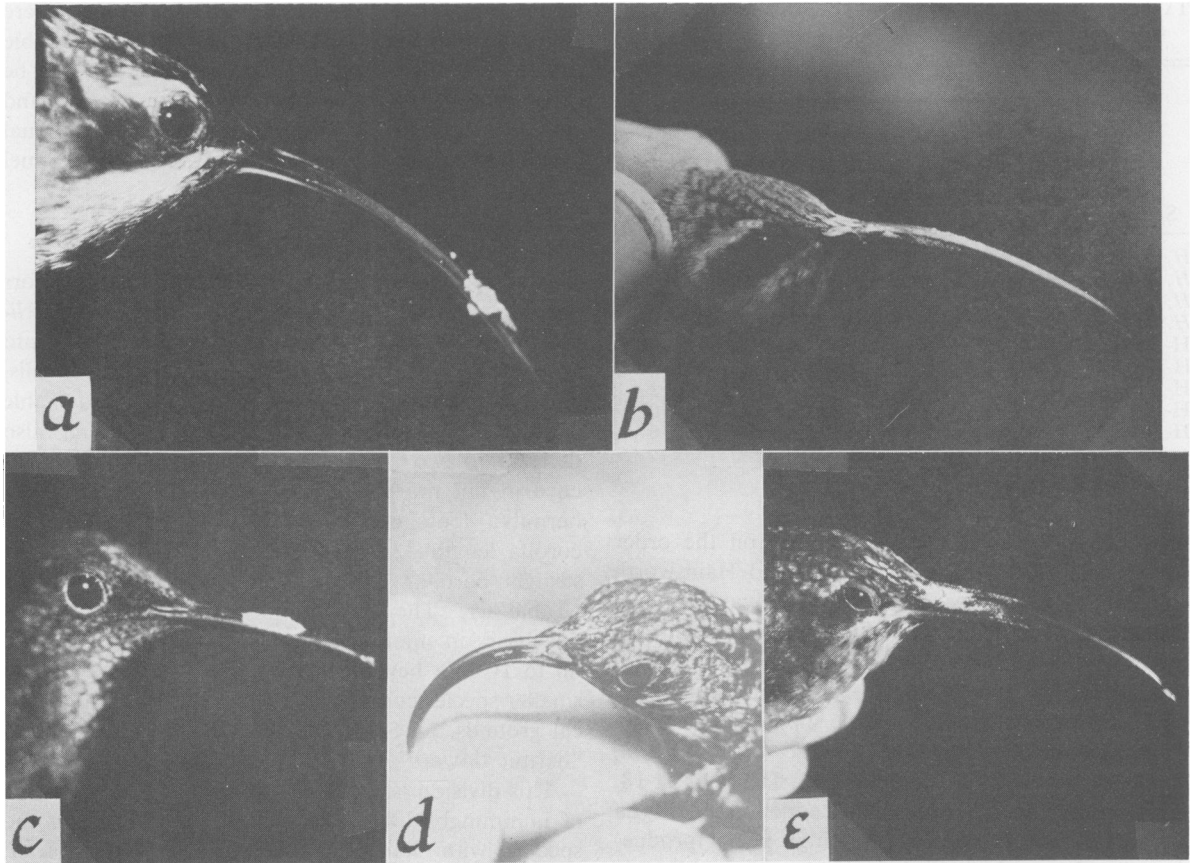Several species showed differences in the timing of

FIG. 7. Deposition sites of pollen of different *Heliconia* species on certain hummingbirds: (a) *H. imbricata* pollen on *Phaethornis superciliosus,* (b) H-18 (forehead, base of maxilla) and H-17 (side of maxilla) pollen on *Phaethornis superciliosus,* (c) *H. imbricata* pollen on *Thalurania furcata,* (d) *H. pogonantha* pollen on *Eutoxeres aquila,* (e) *H. pogonantha* pollen on *Glaucis hirsuta.*

flower and inflorescence production between two successive blooming seasons (Fig. 4). In particular, several species that reach their peak of flowering in the rainy season did so earlier in 1972 than in 1971; this was most pronounced in species that bloomed later in the season in 1971. Thus, *H. imbricata,* H-16, and H-18 reached peak bloom in late July 1972, compared to middle to late August 1971; H-17 peaked in August 1972 and October 1971; and H-3 in August 1972 and late October 1971. *Heliconia mariae* showed less synchrony in production of inflorescences, and less flowering in 1972 than in 1971, but as only two clumps are involved the data are not entirely equatable with data for other species. *Heliconia wagneriana* and *latispatha* attained peak bloom at about the same time in both years, and for *pogonantha* insufficient data are available to compare two successive flowering peaks.

The only species to show pronounced year-to-year variations in other aspects of flowering phenology was H-17. In 1971 relatively few plants produced inflorescences, and many inflorescences produced few or no flowers (Table 4). However, in 1972 this species flowered much more normally for the genus.

Nectar production

Amount, concentration, and caloric content of the nectars of La Selva *Heliconia* flowers are presented in Table 5. This information makes it possible to express the blooming season data (Fig. 4) in caloric terms (Fig. 5). The *Heliconia* species making the largest amounts of calories per clump available to hummingbirds over the longest period are *mariae* and *pogonantha,* although the relative caloric production of *mariae* is probably somewhat overestimated since both of the available clumps are large (Table 2). The caloric outputs of these species are approached or exceeded seasonally by those of *wagneriana,* H-17, and especially *imbricata* and *latispatha.* H-3, H-16, and H-18 nectars make available considerably fewer calories, even at their respective peaks of bloom.

To better understand these data from the birds' point of view, consider that the daily energy require-

TABLE 5. Caloric parameters of the nectars of La Selva *Heliconia* flowers

Species	Approx. daily nectar secretion per flower (μl)	Nectar concentration (M sucrose)[a]	Calories per flower per day (1M sucrose = 1.35 kcal/ml)
H. wagneriana	90	0.95 (0.92–1.00)	0.116
H. imbricata	85	0.65 (0.57–0.73)	0.077
H. latispatha	75	0.90 (0.86–0.93)	0.091
H. mariae	45	0.79 (0.74–0.83)	0.048
H-2	115	0.95 (0.85–1.06)	0.141
H-17	110	0.75 (0.65–0.82)	0.111
H-3	70	0.75 (0.63–0.81)	0.071
H-18	65	1.02 (0.98–1.06)	0.090
H-16	70	0.80 (0.66–0.91)	0.076

[a] Mean and range; N between 5 and 8.

ments of 4- to 6-g hummingbirds are on the order of 6–12 kcal (cf. Stiles 1971, Wolf and Hainsworth 1971). Large clumps of most La Selva *Heliconia* may contain 3 or 4 times more calories than the mean values for 10 census clumps of various sizes given in Fig. 5. Therefore, most or all of a hummingbird's daily energy needs could be supplied by a single clump of *H. wagneriana, imbricata, latispatha, pogonantha*, and H-17, but not H-3, H-16, or H-18.

The daily pattern of nectar production of all La Selva *Heliconia* is similar: very high nectar production in the early morning (with a considerable amount already available when the flowers open at dawn), then a rapid decline to low levels by midday (Fig. 6). The timing of the decline varies somewhat between species, and some show a pronounced "shoulder" of fairly high nectar production around

midmorning (e.g., *wagneriana*, H-16, H-17). There is considerable variation in amount of nectar available at any given time of day. Nectar production can be affected by many factors, including insolation and other microclimatic factors, and the nutritional status of the plants themselves (Huber 1956, Shuel 1966).

Floral morphology and hummingbird visitation

Nine species of hummingbirds are frequent visitors to, and pollinators of, at least one species of *Heliconia* at La Selva. These hummingbirds fall into two groups: the hermits, with long curved bills, and non-hermits, with shorter straight bills (Table 3, Fig. 7). Flowers of La Selva *Heliconia* also divide into two groups, corresponding to the difference in bill morphology between hermits and non-hermits: long and/or curved corollas (effective corolla length 33 mm or more), and short and/or straight corollas (effective length 32 mm or less) (Table 6). The correspondence is even closer if one bears in mind that the tongue can be extended up to 10 mm beyond the tip of the bill in even the smaller species considered here. Thus, on morphological grounds, La Selva *Heliconia* can be divided into "hermit flowers" and "nonhermit flowers."

This division is supported by the observed patterns of hummingbird foraging (Table 7). All five of the species with long, curved corollas (*wagneriana, pogonantha*, H-3, H-16, H-18) are visited to a significantly greater extent by hermits. Three of the four species with short and/or straight corollas (*imbricata, latispatha*, H-17) show a significant majority of visitation by non-hermits. Both bird groups foraged at *mariae*, but data from only two

TABLE 6. Morphology and pollen deposition of flowers of La Selva *Heliconia*

Species	Total corolla length (mm)	Effective corolla length (mm)	Corolla curvature	Site of pollen deposition on Hermits	Site of pollen deposition on Non-hermits
H. wagneriana	65 (59–68)[a]	48 (41–52)[a]	slight to moderate	forehead, crown	not visited
H. imbricata	27 (25–28)	21 (19–23)	slight to moderate	distal ½ to ¼ of maxilla	distal ½ of maxilla
H. latispatha	45 (43–48)	32 (29–34)	nearly straight	½ to ⅔ of way up bill from tip	basal ½ of mandible, chin
H. mariae	28 (25–31)	22 (20–25)	very slight	middle ½ of maxilla	basal ½ of mandible
H. pogonantha	41 (37–44)	33 (30–35)	fairly strong	basal ½ of maxilla, forehead	forehead, crown
H-17	38 (35–40)	28 (25–31)	straight with kink at base	distal ½ to ⅔ of bill	basal ½ of mandible, chin
H-3	53 (50–56)	41 (38–44)	slight	crown, forehead, base of maxilla	not visited
H-18	52 (40–61)	44 (38–50)	slight to moderate	crown, forehead, base of maxilla	not visited
H-16	48 (45–50)	40 (36–45)	slight	chin, base of bill	not visited

[a] Mean and range, $N = 10$.

TABLE 7. Records of hummingbird foraging and territoriality at different *Heliconia* species[a]

| | Hummingbird species (as listed in Table 3) | | | | | | | | | Foraging | | |
| | Hermits | | | | Non-hermits | | | | | Total: Hermits | Total: Non-hermits | χ^2[b] |
Species	E. a.	P. s.	T. r.	G. h.	C. u.	T. f.	A. t.	A. a.	F. m.			
H. wagneriana	0,0	36,2*	3,0	10,1*	0,0	0,0	2,0	0,0	0,0	49	2	43.3**
H. imbricata	0,0	22,0	11,0	12,0	59,41	83,76	40,36	25,2*	27,4	45	235	128.8**
H. latispatha	0,0	7,0	1,0	10,0	20,3	35,13	67,42	16,1	7,1	18	145	98.9**
H. mariae	0,0	2,0	5,0	6,1*	0,0	8,3	9,3	1,0	0,0	13	18	0.84
H. pogonantha	20,3*	73,3*	16,0	70,1*	61,34	24,7	12,2	5,0	3,0	179	105	19.3**
H-17	0,0	14,0	3,0	1,0	23,6	43,16	0,0	0,0	0,0	18	68	29.1**
H-3	0,0	27,0	1,0	14,0	2,0	1,0	1,0	0,0	0,0	42	4	31.4**
H-18	0,0	50,4*	3,0	10,0	1,0	0,0	1,0	0,0	0,0	63	2	57.4**
H-16	0,0	21,1*	2,0	0,0	0,0	0,0	0,0	0,0	0,0	23	0	23.0**

[a] First figure of each pair = foraging records; second figure = records of territoriality. Territoriality figures with an asterisk denotes instances of short-term aggressiveness, rather than true territoriality (see text).
[b] Null hypothesis states equal visitation by hermits and non-hermits. All values with double asterisk are highly significant $(P < .01)$.

isolated clumps may not be properly representative for the species. Non-hermits also hold territories much more frequently at *Heliconia* with short, straight corollas (Table 7). Hermits seldom hold flower-centered territories, and even then these territories are inconsistently defended and are generally at flowers not used by non-hermits. The major exception appears to be at *pogonantha*, where *Chalybura* feeds and holds territories fairly regularly.

In addition to the length and curvature of a flower, its orientation in the bract is important in determining the position a hummingbird must take to feed. This in turn will determine where on the bird pollen from a given *Heliconia* species will be deposited (Table 6, Fig. 7). The flowers in Fig. 1 are shown in their normal orientations within their respective bracts. It is evident that hummingbirds with long, slightly to moderately downcurved bills should have no trouble reaching the nectar in flowers of *pogonantha*, H-3, and H-16. The length and curvature of a flower of H-18 also seem ideal for a hermit, but its orientation forces the bird to rotate its head more than 90 degrees in the vertical plane to insert its downcurved bill (the flower of *wagneriana* is similar in this respect). The pollen of these "hermit" flowers is always carried at the base of the bill or on the head of the bird. The straight-flowered *Heliconia* (*latispatha*, H-17) may be entered easily by straight-billed hummingbirds near the point where the epaxial petal diverges from the corolla tube (Fig. 1). The bird's bill is then above the anthers, and pollen is deposited on its mandible and chin. The flowers of *imbricata* and *mariae* are somewhat curved, but the path to the nectar is relatively short and straight, allowing easy access by straight-billed birds; pollen is deposited on the bills. The flowers of H-3 and *imbricata* are unusual in that they are rotated 180 degrees relative to flowers of other *Heliconia* with erect inflorescences (*latispatha*, H-16,

H-17, H-18). The epaxial petal thus diverges from the corolla tube downwards, as it does in pendant species (*pogonantha* in Fig. 1). This results in pollen being placed on the dorsal side of the bill or head of the bird, compared to the ventral side for *latispatha*, H-16 and H-17. *H. wagneriana* and H-18 accomplish this by in effect rotating the bird rather than the flower.

DISCUSSION
Adaptations for territorial vs. traplining pollinators

Evidence from both floral morphology and hummingbird foraging suggests a dichotomy within the genus *Heliconia* between hermit and nonhermit flowers (Linhart 1973); this may also occur in other groups of hummingbird-pollinated flowers (Snow and Snow 1972). One major behavioral difference between hermits and non-hermits is that the latter frequently hold territories at *Heliconia*, whereas hermits do so only rarely and inconsistently. The energetic feasibility of territoriality for the bird depends on the balance between the energy gained through exclusive or preferential access to the nectar, and the energy expenditures of foraging and defense (Brown 1964, Stiles and Wolf 1970, Wolf et al. 1972). An alternative feeding strategy is "traplining" (Janzen 1971 and *pers. comm.*), which consists of birds traveling between clumps of flowers, presumably following a regular route and visiting the clumps in a particular sequence. All the evidence to date indicates that it is the main strategy of flower exploitation employed by hermit hummingbirds (Stiles and Wolf, *unpubl. data*, Snow and Snow 1972). From the bird's point of view, the flower sources along a trapline must supply enough nectar to be worth revisiting, but not enough to be worth defending (cf. Heinrich and Raven 1972).

Various aspects of flowering phenology favor territorial or nonterritorial hummingirds: the amount

of energy available, the time over which it is available, and its accessibility. The total amount of nectar available in a *Heliconia* clump can vary with size of clump, degree of synchrony of flowering of different plants, rate of flower production per inflorescence, and rate of nectar production per flower. A copious, concentrated, and/or easily accessible nectar may favor territoriality; smaller amounts of dilute, inaccessible nectar, traplining. Nectar concentration can also affect forager size, since relatively dilute nectars can be exploited somewhat more efficiently by small hummingbirds than by large ones, other things being equal (Wolf et al. 1972).

Heliconia imbricata, H. latispatha, and H-17 appear preeminently adapted to pollination by territorial hummingbirds. They frequently grow in large clumps and show both highly synchronous flowering and a high rate of flower production (Table 4). At peak bloom, a clump can produce sufficient nectar to satisfy most or all of a hummingbird's daily energy requirement (Fig. 5). The corollas of these species are short and/or straight, and daily nectar production is fairly high. *Heliconia imbricata* produces a relatively dilute nectar and therefore fewer calories per flower, which might favor the smaller *Thalurania furcata* over the larger *Chalybura urochrysia* and *Amazilia tzacatl* (Tables 3, 7). The nectar of these three *Heliconia* species is also accessible to hermits, which may regularly visit small, isolated, undefended clumps and less frequently try to poach from larger, defended clumps. Were it not for the territoriality of the non-hermits, hermit utilization of these *Heliconia* might well be considerably greater.

Specialization for hermit pollination is shown by H-3, H-16, and H-18 not only in their corolla morphology (Fig. 3), but in their caloric phenology as well. Not even at peak bloom does an average clump of these species contain enough calories of nectar to satisfy a bird's nectar requirements (Fig. 5); thus they favor traplining hummingbirds (cf. Heinrich and Raven 1972). This is achieved through low rates of flower production per inflorescence, and generally small clump size (H-16, H-18) or lack of synchrony of flowering of different plants in a clump (H-3). Daily nectar production of these species is low (H-18) to moderate (H-3, H-16); nectar concentration is moderate (H-3, H-16) to high (H-18), perhaps reflecting the moderate to large size of the hermits themselves (Table 3). By contrast, the specialization for hermit pollination of *wagneriana* appears to be exclusively in its corolla, much the longest of any La Selva *Heliconia* (Table 6). This species often occurs in large clumps, shows synchronous flowering, has a moderate rate of flower production per inflorescence, and secretes a large amount of nectar per flower.

Heliconia pogonantha appears to be primarily hermit-pollinated, at least in forest habitats where it nearly always occurs in small, scattered clumps. Under these conditions, its high nectar production, fairly high flower production per inflorescence, and moderate degree of synchrony of blooming of different plants (if only because individual inflorescences are so long-lived) generally do not result in a concentration of resource great enough to support territorial hummingbirds. Its nectar-rich, strongly curved flowers may reflect specialization for pollination by the large *Eutoxeres aquila*, the only hummingbird to visit exclusively only one species of *Heliconia* (Table 7). However, in second growth, dense populations with many large clumps may occur. *Chalybura urochrysia* is the most frequent territorial species at *pogonantha* under these conditions; perhaps its somewhat longer bill (Table 3) enables it to negotiate the corolla better than can other territorial species. Thus, to some extent the frequent utilization of *pogonantha* by *Chalybura* (Table 7) may reflect human disturbance.

On the other hand *H. mariae* may be adapted for pollination by small territorial hummingbirds like *Thalurania*. The long-lived inflorescences (thus considerable synchrony of flowering), the high rate of flower production per inflorescence, and the short, relatively straight corolla all favor territorial hummingbirds, while the very low nectar production per flower and fairly dilute nectar may favor smaller species. I have found relatively dense populations of *mariae* in northeastern Nicaragua and along the Caribbean coast of Costa Rica being visited mostly by territorial *Thalurania*. At La Selva, it is only near the peak of blooming that the two isolated clumps produce enough nectar to support territorial hummingbirds (Fig. 5). At other times, *mariae* is visited largely by hermits.

Linhart (1973) has shown that hummingbird territoriality can greatly decrease pollen flow to and from the defended clump. Since a *Heliconia* clump is a single individual genetically, this amounts to increasing self-pollination at the expense of cross-pollination, which may be disadvantageous if the *Heliconia* is self-incompatible to any great extent (cf. Levin and Kerster 1971). For a relatively self-compatible *Heliconia*, having a territorial bird in residence may increase the probability that every flower in the clump will be visited, especially if the hummingbird can keep track of which flowers in its territory it has visited most recently, and visit other flowers on its next feeding flight. I have evidence that at least some hummingbirds can do this. Hence, if a self-compatible *Heliconia* has a territorial hummingbird the result can conceivably be a higher fruit

set. The degree of self-compatibility of a *Heliconia* species may thus select for phenology favoring territorial or nonterritorial hummingbirds. No data are yet available on the relative degree of self-compatibility of La Selva *Heliconia*.

Light gaps and pollination systems

The size and permanence of the light gap required by a *Heliconia* species may directly affect the pattern of vegetative growth and clump formation. This in turn can have pronounced effects in flowering phenology, and may restrict the possibilities of specialization for pollination by territorial or traplining hummingbirds. The severe vegetative competition in young second growth probably favors rapid attainment of large clump size in *H. wagneriana*, *imbricata*, and *latispatha*. A high reproductive rate and self-compatibility are also frequently selected for in plants of early successional habitats (Baker 1961). In *Heliconia* this amounts to selection for pollination by territorial hummingbirds, such as occurs in *H. imbricata* and *latispatha*. Hermit pollination in *H. wagneriana* may reflect a lack of self-compatibility in that species. With territorial species effectively excluded by corolla morphology, simultaneous flowering may not be disadvantageous and may make the individual clumps easier for hermits to locate. The main evolutionary risk run by a self-incompatible *wagneriana* would then be the development of a territorial hermit.

Under the forest canopy, low light intensity may make it difficult for a species like H-16 to photosynthesize the metabolic reserves necessary for flowering. I have repeatedly observed whole clumps going through two blooming seasons without flowering. Some plants may never flower, but simply continue photosynthesis until the clump has accumulated enough reserves to permit one of its plants to put out an inflorescence. In H-16, energy may be sufficiently limiting that allocation of reserves to vegetative growth or flowering would be mutually exclusive; hermit pollination is probably obligatory, since a clump can never put out enough nectar to attract a territorial hummingbird. The one forest-based *Heliconia* that does support territorial hummingbirds, H-17, is dependent upon light gaps where presumably enough energy is available to permit both vegetative growth and profuse flowering. In this respect, H≐17 probably resembles the second-growth species mentioned in the preceding paragraph. H-18 is intermediate: at very small light-gaps, clumps are small and relatively few plants flower; at larger light-gaps, or in second growth, larger clumps with a high proportion of plants that flower are the rule.

Given the energetic problems of producing large amounts of flowers inside the forest, it may be no coincidence that H-16 and H-18 bloom simultaneously (Fig. 4). The main effect of this may be to increase the overall level of nectar resources there, so that hermits may more frequently extend their foraging routes through the forest itself; at other times of the year, their major flyways are along stream courses or other large breaks in the forest canopy. Perhaps the uncommon H-16 is in effect making its own clumps more accessible by converging in blooming seasonality with the common H-18. Heinrich and Raven (1972) noted that simultaneous blooming effectively decreases, in a caloric sense, the distance between clumps.

Isolating mechanisms

Since the La Selva *Heliconia* are presumably closely related, selection against hybridization and consequent gamete wastage may be expected. Such selection could occur at the level of the plant population, or that of the flower itself. The former would act to reduce the temporal and spatial overlap in flowering between species (Levin and Anderson 1970). With the exception of H-16 and H-18, the hermit-pollinated *Heliconia* of La Selva show a pattern of sequential and nonoverlapping peaks of flowering (Fig. 4). Among the *Heliconia* pollinated by non-hermits at La Selva, the major divergence has been spatial rather than temporal. H-17 occupies the most shaded habitats, *imbricata* habitats of intermediate light intensities, and *latispatha* the most open areas, often in full sun. A corresponding difference in habitat preference occurs in the hummingbirds, which may have resulted in a partitioning of pollinators. The main visitor to *latispatha* is *Amazilia tzacatl*, which also prefers very open habitats; *imbricata* and H-17 are visited mostly by the shade-loving *Chalybura* and *Thalurania*. Appreciable habitat overlap occurs only between *latispatha* and *imbricata*, and then mainly in second growth (Table 2); these are also the sites where *imbricata* is most visited by *Amazilia*, and *latispatha* by *Thalurania* and *Chalybura*. Human influences have probably caused a breakdown in habitat isolating mechanisms, and these are the only two La Selva *Heliconia* that hybridize to any extent. These hybrids are over 99% sterile, and selection against interspecific pollinations should be strong. The out-of-season flowering of *H. latispatha* (Fig. 4) may represent the early stages of selection for a divergence in blooming seasons between *latispatha* and *imbricata*.

Floral isolating mechanisms may be either mechanical (morphological specializations that impede interspecific pollen transfer) and/or ethological (adaptations that increase specificity of flower choice by pollinators) (Levin 1971 and included references). Among La Selva *Heliconia*, mechanical isolation is

probably accomplished by deposition of pollen of different species in different places on a given type of hummingbird (Table 6; Fig. 7). The flowers of H-16 and H-18 may reduce or eliminate interspecific pollen transfer in this manner, and the same kind of difference is seen between *latispatha* and *imbricata*. In the latter case, this difference is apparently insufficient to prevent hybridization when other isolating mechanisms break down. The species most similar in site of pollen deposition are isolated, at least in part, by habitat (*latispatha* and H-17, *wagneriana* and *pogonantha*) or blooming season (*wagneriana, pogonantha,* and H-3).

Ethological isolating mechanisms are essentially visual and caloric. Visual mechanisms include all the various difference in color, form, and aspect of the inflorescences of different *Heliconia* (Table 1). At the level of the individual forager these factors probably do increase flower specificity. For example, in several instances where two or three *Thalurania* or *Chalybura* individuals held territories at adjacent or interdigitating clumps of *H. latispatha* and *imbricata,* the territorial boundaries always followed precisely the border between the two *Heliconia* species. One *latispatha* inflorescence that projected well into an *imbricata* clump was used and defended by the bird occupying the adjacent *latispatha* clump, rather than the one that held the *imbricata*.

The caloric parameters that may serve as ethological isolating mechanisms include all those factors affecting the ability of different hummingbirds to extract nectar from different *Heliconia*: the length and curvature of the corolla, and the amount and concentration of the nectar. Differences in foraging efficiency of several hummingbirds at different *Heliconia* flowers have been demonstrated (Wolf et al. 1972), and these often correspond to differences in flower choice (e.g., *Thalurania* vs. *Phaethornis* at *imbricata* and *pogonantha*: Table 7).

Competition vs. partitioning of pollinators

Linhart (1973) suggested that the dichotomy between hermit and nonhermit flowers in *Heliconia* may reduce competition for food among the birds, as well as competition for pollinators by the plants. However, with many hummingbirds and few flowers, severe food competition among the birds will coincide with little competition for pollinators among the plants; with many flowers and few hummingbirds, the reverse should occur. Thus the two types of competition may be inversely related, depending on the relative numbers of birds and flowers. At different times and in different habitats, both situations may occur in the La Selva hummingbird-*Heliconia* community.

Competition for pollinators should tend to produce

sequential nonoverlapping blooming seasons (Levin and Anderson 1970); the effect might be difficult to separate from that of selection against interspecific gene flow. Thus, the divergence in blooming seasons among hermit-pollinated *Heliconia* at La Selva could be in part a result of competition for pollinators. A comparable situation, also ascribed to competition, occurs in bat-pollinated plants of both Old and New World tropics (Allen 1939, van der Pijl 1956, Baker 1963, Salas 1973, P. Opler, *pers. comm.*). The overall effect is to provide the large, long-lived bats with a year-round food supply that may help to maintain their residence in the community (Baker 1963). The hermits are the only La Selva hummingbirds that are highly dependent on *Heliconia* flowers at all times of year. Only during the early wet season do the non-Hermits seem to depend on *Heliconia*; at other times of year, other flowers are used.

If the number of potential pollinators is large in relation to the amount of *Heliconia* available, then competition for pollinators may be less important than partitioning of pollinators. Caloric parameters can provide a means of effecting pollinator specificity if several species of hummingbirds and *Heliconia* are simultaneously present. For the hummingbirds, flower specificity should be most advantageous when overall nectar availability is greatest (Wolf et al. 1972, Emlen 1966). Selection for pollinator specificity therefore could result in convergence of blooming peaks between sympatric *Heliconia*. This may have occurred in *imbricata* and *latispatha* since *Thalurania* is more efficient at extracting nectar from *imbricata, Amazilia tzacatl* from *latispatha* (Wolf et al. 1972). In this case, pollinator specificity was probably reinforced originally by habitat selection.

Other sources of selection affecting flowering phenology

Some aspects of flowering phenology may reflect selective pressures arising from sources other than pollination biology. For instance, it appears that temporal partitioning of pollinators by *Heliconia* could be greatly enhanced if different species secreted nectar at more divergent times of day. That the flowers of all La Selva *Heliconia* (and indeed, of all hummingbird-pollinated flowers of wet lowland tropics I have seen) are only half-day flowers may be the result of selection by flower-destroying animals. By late morning, open *Heliconia* flowers are being attacked by insects (*Trigona*, bees, weevils, syrphid fly larvae, ants, etc.) and such birds as tanagers (e.g., *Ramphocelus*) and icterids (*Cacicus*). These animals eat the nectar, often damaging the flower itself, including the ovary. Therefore, exposing a nectar-rich flower for too many hours may

well heighten the chances of discovery by destructive animals. Early morning is probably the best time of day for a flower to expose large amounts of nectar, since the nectar supply can be safely built up at night; most of the dystrophic animals mentioned are diurnal.

Selection arising from fruiting and seed dispersal mechanisms may also influence flowering phenology. For instance, Snow (1965) postulates that the staggered fruiting seasons of Trinidad melastomes is a result of competition for avian dispersal agents (manakins and tanagers). Actually, competition for both pollinators (hermits) and dispersers (chiefly manakins) could occur simultaneously, with both tending toward divergence of reproductive seasons in *Heliconia*.

It should be evident that the adaptation between plant and pollinator in the hummingbird-*Heliconia* system is indeed complex, involving much more than just the morphological fit between corolla and bill. Moreover, as Heinrich and Raven (1972) point out, it is the plant as a whole that is being selected, and its flowering phenology must be seen in the context of selection for other attributes as well.

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