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LONG-TAILED HERMIT HUMMINGBIRD VISITS TO INFLORESCENCE COLOR MORPHS OF *HELICONIA IRRASA*

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ABSTRACT.—Visits by Long-tailed Hermit hummingbirds (*Phaethornis superciliosus*) to flowers of different inflorescence color morphs in a natural population of *Heliconia irrasa* were monitored indirectly using fluorescent powder. The two color morphs (red and yellow) were indistinguishable with respect to amount and rate of reward (nectar) offered to pollinators. The birds did not appear to prefer flowers of either bract color morph. Fluorescent powder was dispersed to flowers of the two color morphs in the frequencies predicted by the relative abundance of the morphs in the study area. This result adds support from field data to earlier experimental work that has challenged the notion that hummingbirds innately prefer red flowers.

Despite the observed association between red-colored flowers and hummingbird pollination, carefully controlled experiments have shown that hummingbirds have no innate color preferences (Bené 1945, Collias and Collias 1968, Stiles 1976, Goldsmith and Goldsmith 1979). Hummingbirds are, however, able to distinguish colors and they readily learn to favor feeders of the color containing the most desirable artificial nectar (Stiles 1976, Goldsmith and Goldsmith 1979). These experimental results have clear implications for the foraging behavior of hummingbirds in nature. Because differences in flower color among plant species are likely to be correlated with floral morphological differences affecting the efficiency of nectar extraction by hummingbirds (e.g., Stiles 1975), pollinator preference for flowers of one species over others cannot be causally related to flower color differences alone. The floral color polymorphisms that are known in many species (reviewed by Kay 1978) provide ideal material for investigation of the role of color in pollinator visitation. In some plant species, the color of flowers or inflorescences changes over time. George (1980) and Schemske (1980) showed that hummingbirds use morphological and color changes to discriminate between first-day, nectar-producing flowers and older, non-rewarding flowers. Interindividual, presumably genetic, floral color polymorphisms are also known in some hummingbird-pollinated plant species. Results from the experimental work cited above predict that hummingbirds will not discriminate between flower color morphs unless the morphs differ in the amount or rate of nectar production. To test this prediction, I studied flowering phenology and nectar production in flowers of two color morphs of *Heliconia irrasa,* and quantified visits by Long-tailed Hermit hummingbirds (*Phaethornis superciliosus*) to flowers of these two morphs.

DESCRIPTION OF THE PLANT

Heliconia irrasa (Heliconiaceae) is a broad-leaved monocot herb found in the understory of wet forests in Costa Rica and Panama. The plants are rhizomatous, but individuals at my study site in Panama rarely have more than two stems and do not form large or dense clumps. During the early wet season (May to June), individual shoots produce solitary erect inflorescences with three to nine large cincinnal bracts. Two distinct colors of bracts and rachises are found among plants at this site (and elsewhere, cf. Daniels and Stiles 1979): pure red ("red-bracted"), and orange-yellow with only the revolute margin of the bract red ("yellow-bracted"). Although yellow bracts tend to become dull and darken with age, the morphs were always readily distinguishable and I found no intermediates. Inflorescences produced from a common rhizome are uniform in color. Although I have no conclusive data, bract color thus appears to be genetically determined. Stiles's observations (pers. comm.) of transplanted rhizomes of this species support this notion.

Each bract contains 8 to 21 flower buds that open one at a time over a period of up to three months. Floral buds are completely enveloped by the cincinnal bracts and even at anthesis only the distal 1 cm of the approximately 6-cm long flower is exposed (Fig. 1). As in most species of this tropical genus, the colorful bracts are thus the most conspicuous portion of the flowering plant. Perianths are solid yellow regardless of bract color. Anthesis occurs at or shortly after dawn and flowers last a single day,

becoming discolored by late afternoon (17:00). Owing to the subtending bract that largely envelops the flowers, perianths wither and decompose in place without falling from the plants. My observations indicated that *Heliconia* flowers at this site were visited by nectar-seeking Long-tailed Hermit hummingbirds. Other long-billed hermit species (*Glaucis hirsuta, Threnetes ruckeri*) may occasionally visit these flowers, but are rare in this area (Ridgely 1976) and I did not see them.

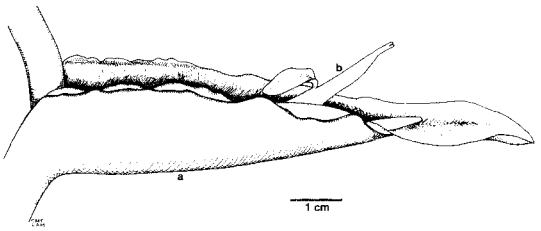

FIGURE 1. Single cincinnal bract (a), with open flower (b), from an inflorescence of *Heliconia irrasa*.

METHODS

This study was conducted in Parque Nacional Soberanía, approximately 10 km NNW of Gamboa, Colón Province, Panama.

All flowering stems of *H. irrasa* were numbered, marked and mapped along a 200-m forested stretch of "Pipeline Road," including an abandoned spur (Fig. 2). In addition to determining the proportion of flowering stems of each color at the site, I made morphological and phenological measurements to test for differences between the morphs. Size of plants (to base of inflorescence), number of cincinnal bracts, and number of flowers produced daily were counted for all marked shoots. The total number of flowers per bract was counted for the basal and distal bracts of a subsample of the study plants of each morph. Cumulative nectar quantity and sugar concentration (sugar weight/total weight) in flowers bagged prior to anthesis were measured every 2 h from 07:00 to 17:00. At least 10 flowers from different individuals of each color morph were used for each sample hour, and I sampled over a two-week interval. Those aspects of data collection that might affect hummingbird foraging (i.e., bagging plants, destruction of bracts to count flowers) were conducted after the experimental portion (see below) of the study was completed.

Three closely spaced red-bracted plants located near the mid-point of the site were chosen for use as the source for marking with fluorescent powder. Between 06:30 and 07:00 on eight days spread through the peak flowering season (July and August) in 1981, an open flower on one of the three plants was marked. The marked flower was on plant 26 except when this plant produced no flowers on a study day. In this case, a flower on plant 55 or 56 was marked (see Fig. 2). The upper sepal of the selected flower was opened gently and orange fluorescent powder (color code A-14-N, Day-Glo Color Corp.) was dusted liberally over the anthers using a pipet. Foraging hummingbirds did not appear to discriminate between marked and unmarked flowers. My observations indicated that hummingbirds visited the marked flower as frequently as other open flowers in the vicinity. I removed all open flowers on all *Heliconia* stems at the site between 13:00 and 15:00 on each of the experimental days. The one or more flowers from each stem were placed in separate, appropriately numbered bags. Each flower was then inspected in the laboratory under ultraviolet light with a 10× lens and scored as being with or without fluorescent powder. No attempt was made to quantify either the amount of powder placed on the source flower or the amount of powder on recipient flowers. Because little is known about the dynamics of powder pick-up, carry-over or deposition, it is not clear that any monotonic relationship between powder quantity and number of visits can be expected. I thus interpreted the presence of powder on a flower as conservatively as possible: any flower that had powder must have received at least one hummingbird visit during the experimental period.

At the end of the study, the limits of the area to be used in data analysis were set at the plants farthest from the sources that received powder during the study. Thus, although stems beyond 75, 47 and 51 at all extremes of the "transect" were originally included in the study, flowers from these stems were excluded from the analysis (Fig. 2). This adjustment should allow hummingbird foraging patterns and the dynamics of transport and deposition of fluorescent powder to set the relevant patch size for this experiment. Within this area, if hummingbirds did not discriminate between morphs, then flowers could be expected to receive powder in proportion to the relative abundance of the color morphs. Flowers beyond this area did not receive powder but I have no evidence that powder can ever be transported so far from the source plant in this system and thus cannot relate the observed absence of fluorescent powder to lack of pollinator visitation.

Expected frequencies of flowers of each morph receiving powder were calculated from the overall proportion of flowers of each morph collected from within the area of observed

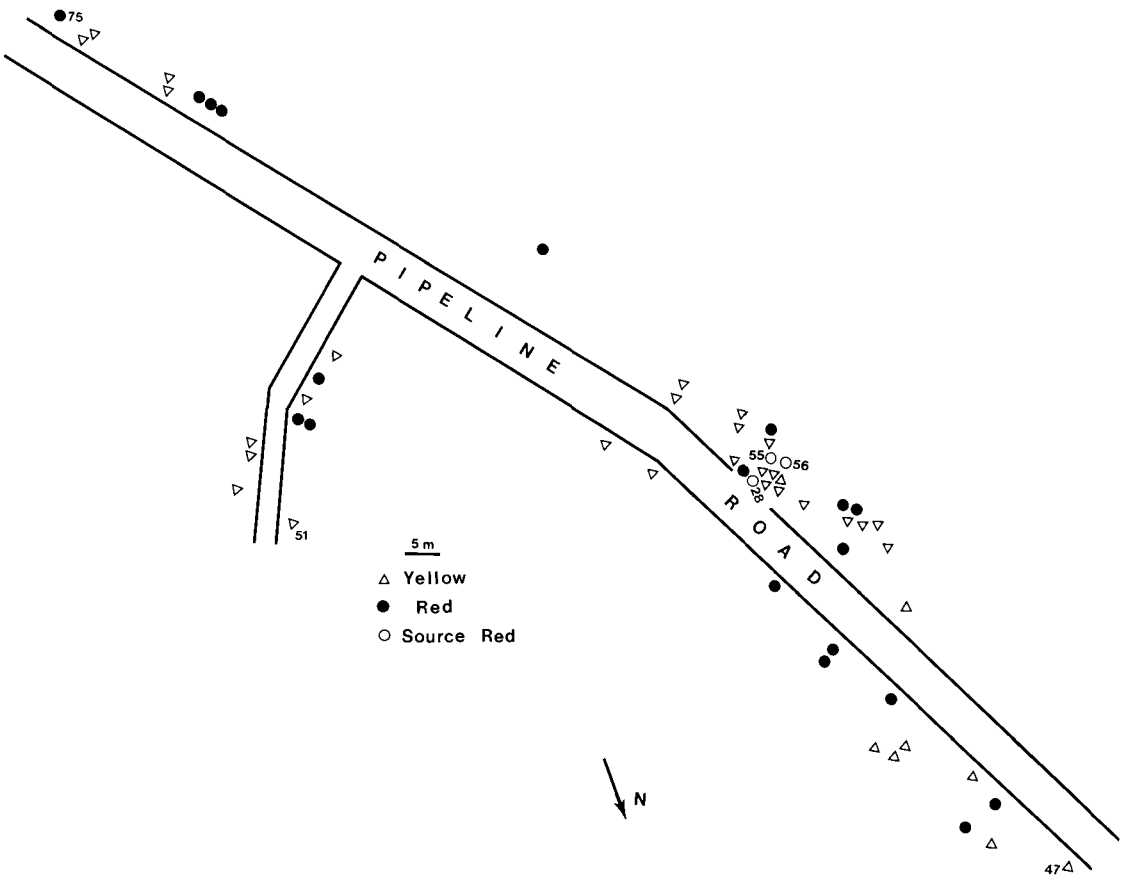

FIGURE 2. Map of study site. Locations of all flowering stems of each bract color morph of *Heliconia irrasa* indicated by symbols. Numbered open circles indicate locations of three stems used as sources of fluorescent powder. Numbered symbols at extremes of site indicate maximal dispersal of fluorescent powder by hummingbirds.

powder flow on each day. Chi-square analysis was used to test for differences between observed and expected frequencies of flowers receiving powder.

RESULTS AND DISCUSSION

Of the 56 flowering stems in the study area, 21 (38%) bore red-bracted inflorescences. A more extensive survey of 135 stems from adjacent areas yielded an identical result: 51 red (38%) to 84 (62%) yellow. I found no evidence of any spatial association of color morphs. At selected radii (10, 25, 50 and 75 m) from the source plants, the proportion of red- and yellow-bracted stems did not differ from the overall frequencies. The two morphs did not differ significantly with respect to the features of floral presentation and phenology measured (Table 1). Because the number of bracts per inflorescence and number of flowers per bract were indistinguishable for the morphs, the total number of flowers produced by inflorescences

TABLE 1. Morphological and phenological characteristics of flowering in two bract color morphs of *Heliconia irrasa*, mean ± 1 SD. Sample size in parentheses.[1]

	Bract color	
	Red	Yellow
Height (cm)	119.0 ± 31.91 (40)	109.6 ± 21.99 (40)
Number of bracts per inflorescence	5.9 ± 1.23 (40)	5.5 ± 1.24 (40)
Number of flowers per bract:		
Basal	16.6 ± 2.61 (15)	17.3 ± 3.09 (15)
Distal	12.1 ± 3.48 (21)	12.0 ± 3.19 (21)
Number of flowers per day	0.76 ± 0.777 (218 plant-days)	0.77 ± 0.827 (318 plant-days)

[1] Means for each characteristic not significantly different between morphs.

TABLE 2. Quantity (μl) and percent sugar content of nectar in flowers of two bract color morphs of *Heliconia irrasa*, mean ± 1 SD. Sample size in parentheses.[1]

	Sugar content	Sample hour					
		07:00	09:00	11:00	13:00	15:00	17:00
Red	27.6 ± 3.97 (22)	40.5 ± 15.55 (11)	39.8 ± 12.09 (13)	58.4 ± 37.56 (11)	49.7 ± 28.53 (11)	48.1 ± 16.24 (10)	36.1 ± 16.27 (12)
Yellow	27.5 ± 3.66 (17)	27.8 ± 17.82 (11)	39.8 ± 18.86 (10)	46.2 ± 19.49 (12)	47.6 ± 19.03 (10)	52.3 ± 21.14 (10)	44.0 ± 23.47 (13)

[1] No significant differences either among sample hours or between morphs.

of each bract color did not differ. Similarly, the rate of presentation (flowers per day) of flowers did not differ between the two morphs. Nectar content was extremely variable among flowers of both morphs throughout the day (Table 2). Although the data suggest a slight difference in phase of nectar secretion (with flowers on yellow-bracted individuals secreting nectar more slowly in the early morning but continuing to produce nectar later in the afternoon), this trend was not significant. Analysis of variance demonstrated no significant differences among sample hour means within morphs (red: $F_s = 1.737$; 5,62 df; $P < 0.25$. yellow: $F_s = 1.888$; 5,60 df, $P = 0.25$), nor were there any significant differences between the two morphs at any sample hour (e.g., for 07:00, when means were maximally different, $t_s = 1.868$, 20 df, $P > 0.05$). Similarly, mean sugar content of nectar did not differ between the two morphs (Table 2).

As indicated by the deposition of fluorescent powder, hummingbirds visited flowers on red- and yellow-bracted individuals in the expected proportions (Table 3). Observed and expected visits did not differ overall or on any of the eight study days. Thus, I found no evidence that Long-tailed Hermits preferred flowers on either of the two bract color morphs of *Heliconia irrasa*.

In the only study published to date of hummingbird visits to differently colored flowers of the same species, Waser and Price (1981) found that Broad-tailed Hummingbirds (*Selasphorus platycercus*) discriminated against rare white flowers of *Delphinium nelsonii*. Although nectar rewards apparently did not differ between color morphs in this species, pollinators may have difficulty extracting nectar from white flowers. The more common blue flowers have a contrasting white "target" formed by the bases of two petals. No such contrasting center is present in albino flowers and hummingbirds apparently have difficulty orienting correctly to visit such flowers. These results confirm that hummingbirds can learn to discriminate flower colors when there is an energetic basis for doing so. My study further confirms results from experimental work using artificial feeders. As would be predicted based on equal rewards offered by flowers of the two inflorescence color morphs of *H. irrasa*, Long-tailed Hermits apparently visited these flowers indiscriminately. In a similar study of this species in southwestern Costa Rica, Gary Stiles (pers. comm.) observed Long-tailed Hermit visits to flowers on the two bract color morphs and reached the same conclusion: the birds visited red and yellow morphs at frequencies predicted by their relative abundance.

When nectar quality differs among flowers, there is clear adaptive value in the ability to learn to select flowers using spatial position and color as cues. As Collias and Collias (1968) suggested, however, "the ability to learn to shift readily from one blossom color to another" is

TABLE 3. Flowers of *Heliconia irrasa* collected by experimental date. Totals include flowers from red- and yellow-bracted plants. Expected number of flowers with powder from red-bracted plants calculated from overall proportion of red flowers and total number of flowers with powder.

Date	All flowers collected		Flowers with powder			χ^2
	Total	Freq. red	Total	Expected	Red observed	
7/15	22	0.40	8	3.2	4	0.252, $P > 0.5$
7/22	20	0.40	12	4.8	6	0.500, $P > 0.1$
7/31	26	0.23	6	1.4	1	0.149, $P > 0.5$
8/04	23	0.26	10	2.6	4	1.019, $P > 0.1$
8/07	27	0.33	17	5.6	4	0.681, $P > 0.1$
8/20	22	0.40	8	3.2	3	0.046, $P > 0.5$
8/23	28	0.36	14	5.0	4	0.311, $P > 0.5$
8/27	32	0.41	15	6.2	5	0.396, $P > 0.5$
TOTAL	200	0.35	90	31.5	31	0.094, $P > 0.5$

highly adaptive, given that food for hummingbirds comes in flowers of different colors. When there is no energetic basis for discrimination among simultaneously available flowers of different colors (as in *H. irrasa*), hummingbirds can maximize their consumption of nectar per unit foraging time by making such shifts within a single foraging bout. This foraging pattern may involve learning to recognize both colors as cues for food, or learning to ignore color in favor of other cues (e.g., position, appearance, smell).

This study adds field data to the already substantial body of experimental work that has challenged earlier simplistic views of hummingbird-flower relationships as driven by an innate and inflexible preference for red flowers. The emerging overview of hummingbird foraging behavior is complex and involves a variety of discriminatory powers, along with the capacity to learn and react flexibly to spatial and temporal changes in food sources.

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