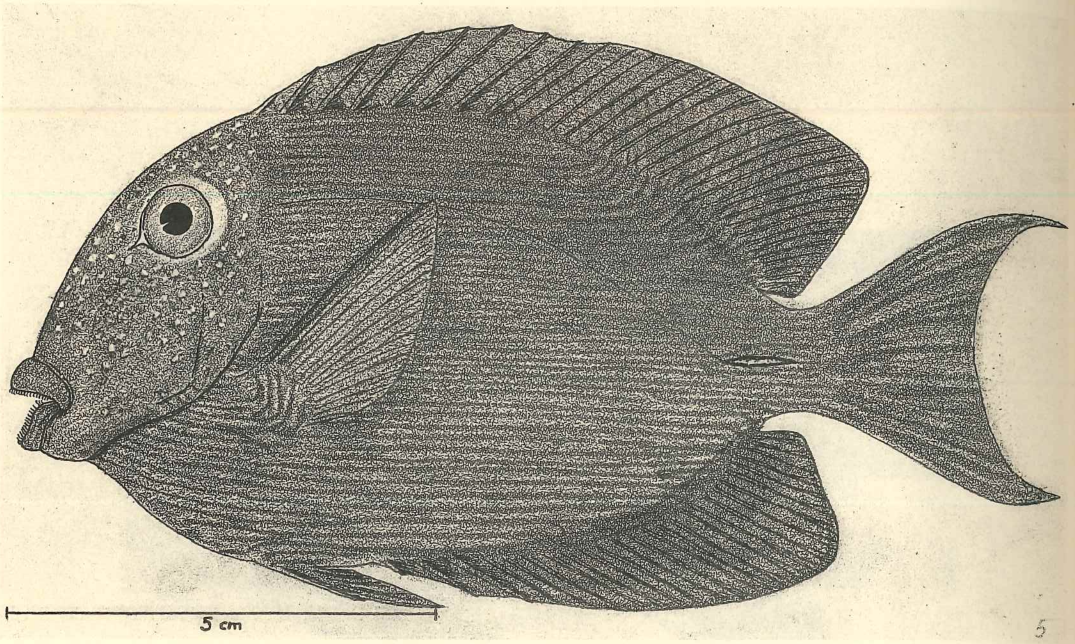

FIG. 1

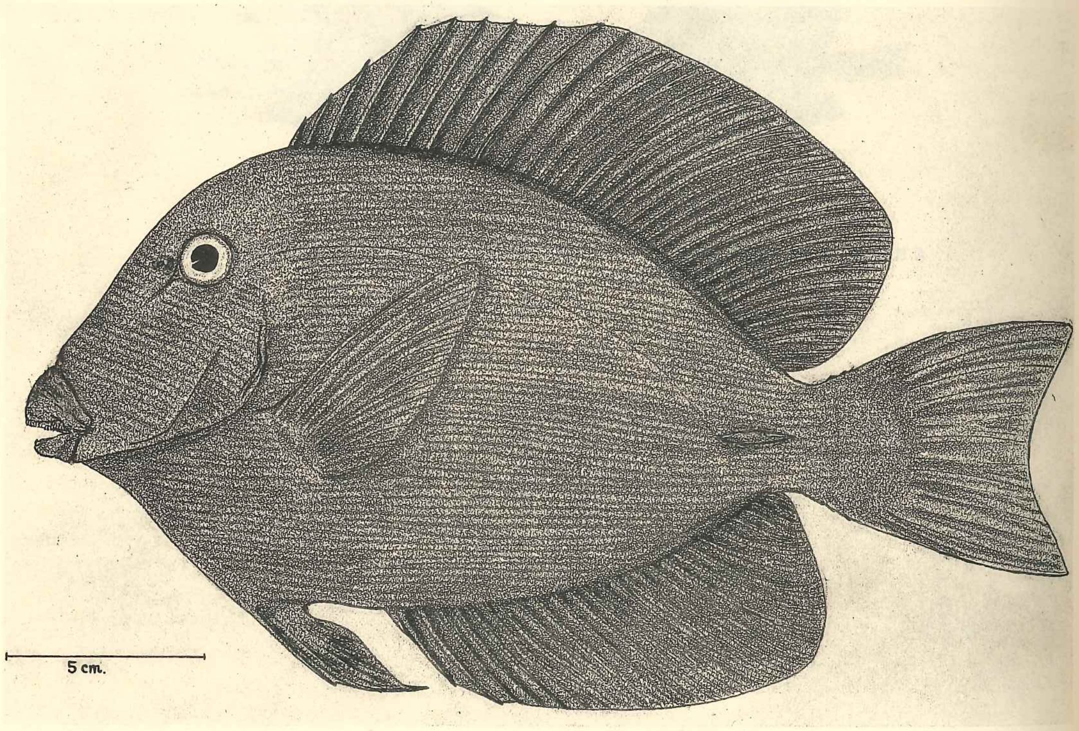

FIG. 2

A REVISION OF THE SURGEON FISH GENUS CTENOCHAETUS, FAMILY ACANTHURIDAE, WITH DESCRIPTIONS OF FIVE NEW SPECIES

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Imaginal Behavior of a Trinidad Butterfly, *Heliconius erato hydara* Hewitson, with Special Reference to the Social Use of Color[1]

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(Plates I-III; Text-figures 1 & 2)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society, at Simla, Arima Valley, Trinidad, British West Indies. This station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.)].

CONTENTS

I. INTRODUCTION

AMONG the most interesting of neotropical insects are the predominantly red and black butterflies occurring in the genus *Heliconius*. Because of the great variety of patterns found in closely related or identical species, the group poses a famous problem in systematics. All of these butterflies are apparently strongly aposematic, and with their basic coloring of scarlet on black, they are considered a classic example of warning coloration. They also serve as one of the most often quoted illustrations of Müllerian mimicry, since the highly variable members of two distinct sections of the genus show many closely similar pairs of forms.

Their general ecology has long been familiar to collectors in the damper parts of the new world tropics. The butterflies are usually common in the various types of rain, montane rain, seasonal and swamp forests. They rarely occur in the depths of the forest itself, however, preferring its edges, glades, clearings, trails and roadsides. They also are typical inhabitants of well-grown open second growth, and of lands devoted to such crops as citrus, cocoa and bananas, provided only that woodland is in the vicinity and that the crops are not too cleanly cultivated.

Except for records of roosting aggregations, it appears that nothing has been published on the social behavior, including the courtship, of *Heliconius*. The purpose of the present paper is to describe and analyze this behavior in the common Trinidad form, *H. erato hydara* Hewitson, with special emphasis on the function of color in in-

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[1] Contribution No. 963, Department of Tropical Research, New York Zoological Society.

traspecific relations. Because of the color variability in other localities and in related sympatric species, the possible role of this characteristic as a social releaser is considered to be of special interest from an evolutionary point of view. This is particularly so because one function of the garish colors is held by many, including the writer, to be aposematic.

In contrast to some continental forms (see especially Beebe, 1955) the Trinidad subspecies is little variable in color or pattern, being black with an unbroken red band running transversely across the middle of the forewing. Except for minor differences in the red, yellow and white dots and bars of head, thorax and basal underwings, macroscopic variation is confined to the irregularities of the margins of the red forewing bands, and to their exact width. A rare local variant has a single tiny red spot, less than 1 mm. across, near the anterior margin of the hindwing. The subspecies, as at present defined, ranges across northern South America from Panama to Trinidad. The species in the broadest sense apparently flies throughout the neotropics from Guatemala south, exclusive of the West Indies.

Because of the emphasis in the present study on the function of color, it was essential to conduct basic experiments on the existence and extent of color perception in this species. These results are included in the present report as prerequisites to the work on social behavior. However, a thorough study of spectral limits, the division of the spectrum into hues, and the precise boundaries between innate and learned aspects of feeding behavior must await further work. A basic remaining requirement is the making of electroretinograms.

Also only briefly treated in the present paper are the three or more odors so far detected in this species, as well as analytical work on roosting behavior.

It is a pleasure to thank the Research Laboratories of the Interchemical Corporation, New York, for contributing spectrophotometric curves of the numerous color samples used in the experiments, and Mr. Ernest C. Crocker, of the Flavor Laboratory of Arthur D. Little, Inc., Cambridge, for his report on the odors of *Heliconius* scent organs.

Deep appreciation goes to Dr. William Beebe, who inaugurated and took part in many of the observations recorded in the following pages. Hearty thanks also go to all members of the Department staff, Dr. Beebe, Mr. Henry Fleming, Miss Rosemary Kenedy and Dr. Richard Tashian, for their help in assembling and rearing specimens, for witnessing key experiments and for many most helpful suggestions.

II. HISTORICAL REVIEW

Butterfly behavior has rarely been systematically observed, much less analyzed by experimental means. A principal exception is a study of the satyrid, *Eumenis semele* (Tinbergen *et al.*, 1941). In this contribution, the feeding and courtship behavior were described, and the respective roles of odor, movement, form and color as feeding and social releasers investigated.

Ilse's pioneer work on butterfly color vision and behavior is also outstanding (1928, 1932.1, 1932.2, 1937). She established beyond question the fact of butterfly color perception through their responses to artificial flowers. The models were made from series of standard gray and colored papers. Differences among the vanessids, pierids and papilionids in innate color preferences were found to occur, and foundations laid for determination of the number and boundaries of the hues distinguished.

Eltringham (1919, 1933) and Eltringham and Ford (Ford, 1945) performed experiments which produced positive responses in *Argynnis euphrosyne* to dyed specimens which had been previously dried and bleached, and to photographic models, painted to resemble living butterflies in color. Their results also indicated that these butterflies respond to color irrespective of motion or odor. However, the spectrophotometric reflectances of the paints and dyes used were not known, nor was hue completely separated from either brightness or pattern. In none of the above studies was the possible role of the ultraviolet investigated.

Similar experiments were carried out by Ilse (1937), by Eggers (1938.1, 1938.2) and by Petersen, Törnblom & Bodin (1952), all of whom worked with pierids. The latter contribution, based on responses of wild polymorphic species to dried specimens and to models, makes a needed beginning on the vital problem of visual releasers in polymorphic butterflies. The role of the low ultraviolet reflectance of white pierid wings remains uncertain (see also Crane, 1954, p. 108 and ref.).

Records of butterfly courtships, mostly descriptions of necessarily incomplete observations in the field, are scattered through the literature, particularly in the field accounts of the older naturalists. Carpenter (1935) gives a general discussion and a good bibliography. Courtships in the heliconines, however, have apparently been hitherto unknown. The only reference to mating behavior appears to be that of Edwards (1884) who reported on males of *H. charithonius* gathering on the chrysalids of females and mating with them on emergence. Territoriality is suggested by Seitz (1913, p. 377) who observed heliconine males "promenading" up and down individual beats in the forest, day after day.

The emission of scent by butterflies, apparently sometimes as sexual attractants and sometimes for protection against predators, has been described from time to time. Notable are Longstaff's (1912) observations, which include descriptions of the strong, witch-hazel-like odor which some *Heliconius* emit when captured (pp. 492, 503-504). Poulton (1925, 1931.2), Longfield (1926) and Collenette (1929) added more details and opinions on the scents of heliconiids, including the subject of this paper. Müller's (1878) descriptions and figures of scent glands and scales in danaids and heliconines are classsics; translations have been published by Longstaff as appendices (*loc. cit.*). Eltringham (1925, 1926) published further studies of both the glands and their odors in *H. erato hydara,* as well as in the genera *Coloenis, Dione* and *Eueides;* these three genera included species now referred to *Dryas, Agraulis* and *Heliconius*. Finally Barth (1953) discussed the form and function of the scent organs of male Lepidoptera from a more generalized and comparative point of view.

Gregarious roosting habits have been reported for a number of butterflies, including representatives of the danaids, heliconiids, ithomiids and nymphalids (e.g. Beebe, 1918, pp. 203 ff.; Myers, 1930; Jones, 1930, 1931; Poulton, 1931.1, 1931.2; Poulton and others, 1933; Guppy, 1932 and Carpenter, 1932). The only experimental work has been that of Jones (*loc. cit.*) who determined that *H. charithonius* in Florida was attracted on successive nights by a general locality recognition of some kind, rather than to special twigs or branches. Hence the attraction was not to an odor left on particular resting places.

Gatherings of various butterfly species on damp sand or around mudholes are also well known (e.g. Collenette & Talbot, 1929), as are the winter aggregations of monarch butterflies, *Danaus plexippus,* as mentioned in, for example, Swain (1948, p. 109). Records of butterfly migrations in all part of the world are exceedingly numerous, the most intensive study having been made by Williams (1930). No migrations of heliconines appear to have been reported, except the occasional flights, small and moderately large, reported at Portachuelo Pass, Rancho Grande, in Venezuela by Beebe (1950).

Food plant selection and the general egg-laying habits of female butterflies have received the widest notice, chiefly because of the frequent economic importance of the subject. Seitz's (1913, p. 377) observations on *Heliconius* seem to be the only field notes for that genus, although the caterpillars are fairly well known. He observed these butterflies near Belém laying eggs on *Passiflora,* usually around noon; they apparently chose high-climbing vines.

A paper on the spectral composition of certain butterfly colors (Crane, 1954) includes an analysis of the red band in *H. erato* which was a prerequisite to the investigation of the band's function in intraspecific relations. It proved to have a minimum reflectance from the ultraviolet through the green, low in the yellow and high in both the orange and red.

III. MATERIALS AND METHODS

Two circumstances permitted the undertaking of the present study. Of first importance was our location in a permanent tropical field station in an area where *Heliconius erato* is common. This contribution is the result of observations and experiments extending over parts of five years. The second factor was our maintenance of two large insectaries for the study of captive butterflies.

The construction and operation of these flying cages have been described elsewhere (Crane & Fleming, 1953). Here it need only be said that the structures measure 12′ × 18′ and 24′ × 36′, respectively, and are built of fine wire mesh on a wooden framework. Being floorless, they are planted with a profusion of herbs, shrubs and vines approximating natural conditions. Ample sun, shade and wind protection are essential as well as the maintenance of high humidity. Butterflies caught in the field are placed in envelopes, kept cool and released in the insectaries as soon as possible.

Heliconius erato proved to be the most amenable to life in the insectaries of numerous species tested. Once these large cages have been "seasoned," presumably through clinging species odors, newcomers settle in at once, feeding and successfully avoiding the wire within minutes of their release. Reared specimens are equally adaptable.

The favorite local food flower of these butterflies is *Lantana camera* Linnaeus; also popular are *Bidens pilosa* Linnaeus and *Verbena* spp. All of these are either grown in the insectaries or provided daily as freshly cut flowers.

Small cubic cages measuring about three feet on each side served to isolate newly emerged imagos in preparation for experimental work. Individuals could be thus kept for about two days without harm to their subsequent vitality, providing that the cage stood in the shade, was partly covered with green branches and was freely sprinkled with water during the heat of the day. *Lantana* was supplied on a shelf six inches below the roof, since butterflies kept in such small spaces do not readily feed from bouquets on the floor. Although mating was once secured in a small cage, normal courtship was absent, and no female was ever induced to oviposit under such conditions.

A description of the growth stages of this species, as well as an account of the rearing technique, is in preparation. Here it is appropriate to mention the general precautions necessary in order to produce the vigorous adults which are essential for behavior study: the larvae must be reared in individual, closely covered containers; provided amply at least once a day with freshly picked, or briefly refrigerated, leaves of appropriate sizes from the vine *Passiflora tuberosa* Jacquin; furnished with suitably high amounts of light and humidity; and kept clean. The chrysalids also must be kept in a humid environment. In short, this is not a species that can be healthfully reared *en masse* in a shoebox.

The experimental techniques employed in the study of vision and of social behavior will be described under the appropriate sections (below and pp. 183-190).

IV. VISION: SPECTRAL RANGE AND COLOR PERCEPTION

In this section will be briefly considered certain characteristics of the visual sense of *Heliconius erato,* with brief mention of other butterflies.

A few experiments were made, as described below, only to establish with certainty that color perception and sensitivity from the near ultraviolet at least to the orange exist in this species and play a role in both innate and acquired feeding responses. Detailed studies of color vision and feeding behavior are reserved for the future.

A. LIMITS OF THE SPECTRUM. From time to time various species of butterflies, including *H. erato,* were tested for responses to light of various spectral characteristics. In each experiment a wooden box was used, measuring either 3′ × 3′ × 2′ or 4′ × 3′ × 3′. Each box was completely light-tight, all cracks and corners being reinforced with black photographic tape, except for the following apertures: One 5″ × 5″ opening in a corner of the top, for covering with a filter which, in turn, was sealed in place with tape; a light-tight door, near the bottom, for insertion of butterflies; a suitably-sized hole for insertion of a flashlight, which was fastened tightly with the switch extending outside; and finally an eye-hole. The latter measured about 1¾ inches in diameter and was fitted with a short length of flexible black tubing; when not in use the exterior end of the tube was covered with a black paper cornucopia. Before every test the box was checked for light-seepage by an independent observer.

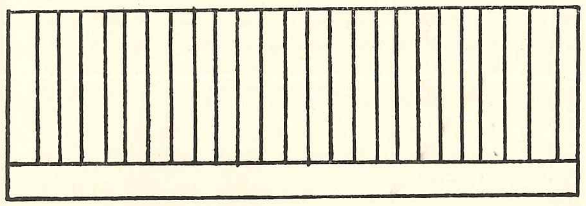
After the introduction of one to three butterflies the box was left undisturbed in the open air for a maximum of five minutes. When the ultraviolet filter was used on dull days, the natural daylight was supplemented by placing a portable ultraviolet lamp close above the filter. After a few minutes, the positions of the insects were observed by means of the eye-hole and, in the case of the ultraviolet filter, by use of the inserted flashlight. The filter was then covered with a piece of wood and, when the observer's hand was inserted through the butterfly entry door, the butterflies were disturbed and forced to seek new positions away from the filter. The same procedure was then repeated twice more with all individuals tested.

In the tests involving *H. erato,* 11 out of 12 specimens individually introduced under each of the filters (not necessarily on the same day) batted against both the Corning Ultraviolet #5860-7-37 and Corning Red #2408-2-60. These filters pass, respectively, no light of wavelengths longer than 390 mμ or shorter than 610 mμ. Most of the responses to the ultraviolet occurred within 30 seconds. Strong positive responses were also obtained to filters transmitting freely in intermediate spectral regions. The following other species were tested with similarly unequivocal results: Heliconiidae: *Heliconius sara* (3 individuals), *H. ricini* (2), *Agraulis vanillae* (3). Danaidae: *Danaus plexippus* (4). Ithomiidae: *Tithorea mopsa* (1). Papilionidae: *Papilio neophilus* (3), *P. anchises* (2), *P. anchisiades* (3). Pieridae: *Eurema albula* (2), *Phoebis sennae* (2), *Anteos maerula* (1).

Although it was expected that butterflies would prove to be sensitive to the ultraviolet, in common with the numerous insects of other orders which have to date been tested, no reports on such responses in Rhopalocera appear hitherto to have been published.

The tests established conclusively that for *H. erato* the visible spectrum extends from at least the near ultraviolet at least up to 610 mμ, which marks the extreme lower transmission limit of the red filter employed. The experiments yield no data at all, of course, concerning the relative brightness for the insect of the various spectral regions, nor do they indicate whether any of these regions are distinguished qualitatively, that is, as different colors.

B. COLOR PERCEPTION. Since existence of a color sense in the heliconiids has never previously been tested, basic experiments were undertaken to determine whether the capacity is present in this family. The same general system was used as that employed by von Frisch and others with bees (von Frisch, 1948, 1950 and ref.), and by Ilse with butterflies (1928). In all of these, colored samples, in our case paper flowers, were offered among a large number of gray samples ranging in brightness from "white" (positively ultraviolet), to "black." No training was undertaken in the present series, since under certain conditions the species came spontaneously to the colors, and since it was only desired to determine whether or not they could distinguish color from any shade of gray, rather than one color from another.



TEXT-FIG. 1. Pattern used in making three dimensional paper flower. The fringed strip is rolled up and fastened at the base with scotch tape and a paper clip. Natural size.

In the present tests, advantage was taken of the tendency of *H. erato* to come to small colored objects of certain forms—i.e., of flower-like shape. As has been shown in bees (von Frisch, 1948, 1950 and ref.) and butterflies (Ilse, 1932.2), the most successful were small circles with fairly numerous converging petal-like divisions. Our most successful models were more complex than those previously described, and strongly three-dimensional. Flat ones, although they evoked a few responses, were far less popular.

Series of these model flowers were fashioned from Stoelting Psychological Test papers in 17 colors, and from papers painted in a variety of opaque water colors and with Floquil paints. All of these were analyzed spectrophotometrically in the visible and near ultraviolet through the courtesy of the Research Laboratories of the Interchemical Corporation.

A series of 20 gray steps was also made, by hand, from highly ultraviolet reflectant blotting paper dipped in a measured succession of progressively higher dilutions of India ink with distilled water. This laborious procedure was necessary because a commercially manufactured gray-step series with the necessary characteristics could not be located. The only one found in the United States (the Munsell series) with a sufficiently matte surface proved upon spectrophotometric analysis to have a very low reflectance in the ultraviolet. In fact some results obtained during one season were misleading until this characteristic was ascertained, since the butterflies came rather freely to some of the lighter grays; apparently for them, as for bees, negatively ultraviolet whites are colored. This never occurred with the India ink series, the only responses to uncolored (for humans) flowers being to a model painted with Chinese white (zinc oxide); as is well known, this substance has minimal reflectance in the ultraviolet, and so, by subtraction, apparently appears colored to the butterfly.

In order to control the possibility that the odor of the India ink was a deterrent to the butterflies or that, conversely, some of the paints or papers had an odor attractive to them, the same ink, in various dilutions, was applied in alternate rows of "petals" on single colored flowers, while bits from the most popular colored flowers were placed invisibly but open to the air beneath as well as within some of the gray models. The butterflies' responses were unaffected. The preference of the butterflies for three-dimensional models made impractical von Frisch's use of a glass plate over flat models.

The technique of the tests was as follows: they were run in two parts. First, a group of experienced butterflies, well settled in an insectary, was deprived of food for a few hours. The best time for tests was between nine and eleven o'clock on a sunny morning; therefore food was usually removed the preceding afternoon. The artificial flowers were displayed in checkerboard fashion on an inverted square tray made of wire netting with a one-quarter- or one-half-inch mesh. The flower models were attached to the meshes by paper clips. They were displayed both with and without basal circles of black paper for contrast, without noticeable difference in the results. Sufficient tests of this aspect, however, have not yet been made which would enable the statement of reliable conclusions.

Freshly picked *Lantana* leaves were used to cover the netting at the base of the models, since experienced butterflies made extremely few responses to models without the added stimulus of odor. Amyl acetate was also used with some success, being sprayed on a pan of damp sand or earth in which the models were set. In half the tests no reward was provided; in the other half, all the models—both colored and gray—were fastened to half-dram vials filled with a 10% solution of white sugar.

TABLE 1. SPECTRAL REFLECTANCE OF PAPERS, PAINTS AND TEXTILES USED IN *Heliconius* EXPERIMENTS.

Explanation: From spectrophotometric curves furnished by the research laboratories of the Interchemical Corporation, New York, N. Y. Sources and general type of the materials used were as follows:

Papers: a. Stoelting Psychological Test series (a smooth-finish matte surface).
b. A series of school construction papers (a rough-finish matte surface).
Paints: a. Floquil "Flopaque" (a quick-drying opaque lacquer).
b. Richart opaque water colors.
c. "Stroblite" fluorescent paint. (Translucent). (Bright pink).
Textiles: a. Light-weight canvas.
b. Heavy, opaque, felt-like cotton.

The papers were used for experimental flowers and markings on butterfly models; opaque lacquer used especially for painting living butterflies, but also for paper flowers; opaque water-colors principally for paper flowers; canvas and felt served as foundations for butterfly models.

Also used were (1) white paper and paint with high ultraviolet reflectance which approached that of wavelengths in the visible; (2) zinc oxide paint with minimal ultraviolet reflectance; and (3) a series of 18 neutral grays, with positive ultraviolet reflectance (see text, p. 171).

			REFLECTANCE (% OF MAGNESIUM OXIDE)																		
			Ultraviolet			Violet			Blue		Blue-green	Green		Yellow		Orange		Red			
			Wave-length (mμ)																		
Sample	Color	Material	340	360	380	400	420	440	460	480	500	520	540	560	580	600	620	640	660	680	700
1	Violet	Paper	18	20	25	26	27	30	28	20	13	7	8	4	5	8	9	11	13	18	25
2	Violet	Paint	33	31	38	43	46	45	36	23	14	9	8	8	9	9	12	19	35	57	74
3	Violet-blue	Paper	9	10	14	19	22	23	22	18	14	11	9	8	7	7	10	17	23	27	33
4	Blue	Paper	9	10	16	35	46	52	51	39	24	14	10	7	6	6	6	7	8	12	18
5	Blue	Paint	8	8	12	23	28	29	28	25	21	17	15	12	11	10	9	8	7	7	7
6	Blue	Paint	52	55	59	56	61	66	64	52	37	24	16	12	11	10	11	12	15	20	28
7	Blue	Cloth	21	24	30	31	35	36	36	33	29	25	21	18	16	15	15	16	17	19	21
8	Blue	Paper	17	20	24	24	25	38	45	46	45	40	30	20	12	9	7	6	8	12	23
9	Blue-green	Paper	10	10	14	23	26	29	35	46	54	53	47	40	32	27	24	22	24	28	32
10	Blue-green	Paint	7	8	14	22	24	25	28	32	33	31	28	25	21	18	16	14	13	12	12
11	Blue-green	Cloth	18	17	15	14	14	16	22	30	34	32	27	22	17	13	12	13	14	16	18
12	Green	Paint	6	6	6	5	5	6	7	11	17	18	15	11	9	8	7	6	6	6	6
13	Green	Paint	14	14	13	11	10	18	18	27	38	38	31	23	17	13	11	9	9	12	18
14	Green	Cloth	8	8	8	7	7	8	11	17	22	23	20	16	12	10	9	9	9	10	11
15	Yellow-green	Paper	14	22	24	20	20	21	24	30	45	56	58	45	40	38	37	38	41	44	48
16	Green-yellow	Paper	13	14	14	13	12	13	15	19	35	61	67	62	55	51	48	46	50	59	69
17	Yellow	Paper	7	7	9	8	9	10	14	25	41	59	67	70	71	71	70	70	72	75	77
18	Yellow	Cloth	9	9	8	9	8	9	11	15	18	34	41	46	50	53	55	58	60	62	64
19	Yellow	Paper	9	9	12	16	17	17	19	26	36	44	51	57	62	66	69	72	74	77	79
20	Yellow	Paint	5	6	6	6	6	6	6	7	9	25	52	65	71	73	74	75	76	76	77
21	Yellow	Paint	8	8	8	8	8	8	9	11	22	50	75	83	84	85	85	86	88	90	91
22	Yellow-orange	Paper	7	7	7	6	7	7	7	7	9	25	54	68	72	74	75	76	77	78	79
23	Orange	Paper	6	5	5	6	5	5	5	6	6	9	10	15	33	58	70	73	75	77	78
24	Orange	Paper	7	9	10	10	10	10	8	7	7	7	9	19	39	55	62	66	69	72	74
25	Orange	Paint	7	7	7	6	6	7	7	7	8	11	17	29	45	61	71	76	78	79	80
26	Orange	Paint	13	12	12	11	10	10	10	10	11	12	14	23	51	75	82	84	85	88	90
27	Orange	Cloth	8	12	10	7	6	6	5	6	6	8	10	22	41	55	60	62	63	65	68
28	Orange-red	Paper	6	6	6	5	5	5	5	6	6	7	7	9	16	39	65	75	78	79	80
29	Red	Paper	6	6	5	4	4	4	4	4	4	5	5	6	8	19	45	65	72	75	78
30	Red	Paper	7	7	10	10	9	8	7	6	5	5	6	7	11	17	26	38	50	59	65
31	Red	Paint	4	4	4	4	4	4	4	4	4	4	5	5	8	13	33	57	67	72	74
32	Red	Paint	15	20	16	16	16	16	13	11	10	9	9	8	18	38	70	82	86	88	90
33	Red	Cloth	3	4	4	3	3	3	3	3	2	2	2	3	4	10	25	40	50	57	62
34	Violet-red	Paper	14	16	22	21	21	23	22	16	11	8	7	6	10	22	45	56	61	64	67
35	Pink	Paper	14	17	18	17	16	16	14	15	11	10	9	11	19	40	64	70	73	75	76
36	Pink, fluorescent	Translucent Paint on White Paper	10	10	15	21	25	31	34	27	22	20	19	20	20	40	63	68	72	75	77

In preliminary tests five models were displayed, representing general spectral regions: blue, blue-green, yellow and orange-red, all except some blues having minimum reflectance in the ultraviolet. As always they were exhibited with the complete series of gray models, plus one of Chinese white. In subsequent tests four models, of roughly similar hues but of varying brightnesses and texture, were displayed among the grays, such as four yellows, or four orange-reds and reds. Generally each test was limited to 15 minutes. Hungry butterflies on bright days would return and probe a paper flower—whether or not sugar water was attached—a number of times; well-fed individuals in cloudy or oppressive weather would give very few or no responses, even though they were repeatedly flushed from resting positions. Responses were divided into three parts (Table 2), "dips," in which the butterfly changed course and fluttered down within three inches of a particular model, alightings and probes; in the latter actual and often vigorous attempts were made to feed, with the proboscis uncoiled; when no sugar water was furnished the attempts were sometimes much prolonged.

Second, inexperienced butterflies, which had never previously fed on or seen any flowers, or even any other butterflies, having been kept in isolation cages (p. 187), were introduced singly into an insectary. Individuals, especially males, allowed to go about fifty-four hours without food upon emergence, sometimes came spontaneously straight over to the experimental tray and probed repeatedly at several differently colored models in succession, a variety of hues being displayed among the grays. These responses were without the added attraction of either *Lantana* leaves or amyl acetate, and no sugar water was provided. In fact, no chemical stimulus was ever employed with the inexperienced individuals; therefore their positive responses were all to visual characteristics alone. However, younger butterflies had to be tested by fastening the test flowers in succession on the end of a stick; the model was then brought, sometimes several times over, slowly up to the head of the resting butterfly. The order of color presentation was varied in different individuals, and with the same individual in different test sessions, without allowing either real food or other insects in the insectary until after the conclusions of the tests.

The results of both these groups of preliminary tests to determine the presence of color vision in *H. erato* were conclusive:

1. Neither experienced nor inexperienced butterflies ever dipped toward, settled on or probed an uncolored paper flower, except for the model painted with negatively ultraviolet Chinese white (zinc oxide).

2. Positive probing responses were obtained for literally all regions of the spectrum, including some with relatively high ultraviolet reflectance, except blue-greens and greens, and by inexperienced as well as experienced butterflies, without the addition of odor. Feeding response to color is therefore innate.

3. The largest numbers of responses were received, in this order, by yellow, orange-yellow, orange and Chinese white. Blue, whether positively or negatively ultraviolet, was next to blue-green and green least popular of the colors. No actual proportions of responses to the different models can be given; the variations of presentation were not made with sufficient care to ensure a random, or other system of rotation, and a given butterfly, or group of butterflies, invariably ceased to respond before an entire series could be run. Table 2 gives an adequate sample of typical series of responses.

4. The preferences held among the inexperienced as well as the experienced and show that the attraction for "yellow" in food is innate and not only a learned association with such favorite food-flowers as *Lantana, Bidens,* etc. It is, of course, by the terms of the experiments, not yet known whether the unpopularity of the blue and green regions is due merely to a low retinal sensitivity. It is interesting to recall that in Ilse's experiments, vanessids—which of her groups are nearest the heliconiids—found the blue and yellow regions of the spectrum most attractive. It will be noted that blue is not a favorite with the heliconiids. The papilionids and pierids on the other hand came most freely to red. Casual but repeated observations in the field, garden and insectaries in Trinidad support this red preference in the tropical papilionids and pierids.

V. BEHAVIOR OF IMAGOS: GENERAL ACCOUNT

A. INTRODUCTION. The following account of the adult behavior of *Heliconius erato* is based principally on the activities of specimens observed in the Trinidad insectaries. However, all the general observations, including food flower preferences, time of day and meteorological conditions governing roost-leaving, feeding, courting, egg-laying and roosting, have been checked a number of times in the field, by other staff members as well as by the author. These checks were found to agree with the more detailed observations made possible by the insectaries.

B. HABITAT AND FLIGHT HABITS. *Heliconius erato* flies typically along the edges of seasonal, lower montane and swamp forests, and of well-established second growth. These characteristic localities occur along roads, open trails, streams and old, small clearings; the butterfly is also common in overgrown citrus and cocoa cultivations. It does not fly in the depths of thick forests, since partial sunlight is an essential. In the Arima Valley it has not been seen above 1,200 feet, although it was fairly common at

TABLE 2. FEEDING RESPONSES OF EXPERIENCED *H. erato hydara* TO 4 COLORED ARTIFICIAL FLOWERS AMONG A SERIES OF 18 GRADUATED GRAYS AND ZINC OXIDE WHITE.

The data below are typical of the results obtained in about twenty similar tests. See text, p. 170 ff. and Text-fig. 1. Numbers under colors refer to samples analyzed spectrophotometrically in Table 1, p. 172.

Test conditions: Five hungry individuals were used in each 15-minute test. No individual had been tested within the preceding five days and all were habituated to insectary conditions. Tests were conducted only on calm, sunny mornings between 9:30 and 11:30 A.M. No food was furnished with the flower models, although *Lantana* leaves were placed evenly around their bases. The models were arranged in the usual checkerboard (Roman square).

In no test was there any response whatever either to models of the gray series, including positively ultraviolet white, or to *Lantana* leaves.

Test a

Responses to Violet, Blue and Zinc Oxide White

	Violet (No. 1)	Violet (No. 2)	Blue (No. 6)	Blue (No. 13)	Zinc Oxide White
Dips	–	–	–	–	–
Alightings	–	–	–	–	2
Proboscis probes	–	1	–	1	2
Total	–	1	–	1	4

Test b

Responses to Blue, Blue-green and Zinc Oxide White

	Blue (No. 5)	Blue (No. 9)	Blue-green (No. 10)	Blue-green (No. 12)	Zinc Oxide White
Dips	1	–	–	–	3
Alightings	–	1	–	–	2
Proboscis probes	–	–	–	–	4
Total	1	1	–	–	9

Test c

Responses to Yellow and Zinc Oxide White

	Yellow (No. 19)	Yellow (No. 20)	Yellow (No. 21)	Yellow-orange (No. 22)	Zinc Oxide White
Dips	2	8	1	13	2
Alightings	–	–	1	2	1
Proboscis probes	16	2	21	6	2
Total	18	10	23	21	5

Test d

Responses to Orange, Red and Zinc Oxide White

	Yellow-orange (No. 22)	Orange (No. 23)	Orange-red (No. 28)	Red (No. 29)	Zinc Oxide White
Dips	7	4	2	1	1
Alightings	1	2	–	–	–
Proboscis probes	9	5	–	–	–
Total	17	11	2	1	1

Rancho Grande, Venezuela, at 3,600 feet. It is a low flier, usually fluttering between about three and seven feet off the ground, and rarely is seen as high as 20 feet. Females, when about to lay, skim along a few inches to two feet above the ground, since the local food plant is usually low-growing.

In the insectaries a combination of ample shade and sunlight is required plus a high humidity and an abundance and variety of growing herbs and shrubs. Given these conditions *H. erato* thrives in captivity better than any of the remaining fifty-odd species so far tested, although all the heliconines do well.

C. Relation of Behavior to Meteorological Conditions. Temperature, light and humidity are all important in the behavior of these completely diurnal butterflies. Temperature is the critical factor which governs their first morning activity, while light intensity controls roosting in the late afternoon. At Simla they are always inactive, regardless of the light intensity, at temperatures lower than 67° F. (19.4° C.); the usual minimum for activity however is 70° F. (21.1° C.). This temperature has never, between December and June, which includes the coolest season, been reached later than 8 A.M. The usual time of first morning activity changes with the seasons. In January it usually occurs between 7 and 8, in April between 6:30 and 7:30, and in May and June the first butterflies frequently leave the roost at 6:45. In hot weather, when the early morning temperature does not fall below 70° F. (21.1° C.), light is the crucial factor. Ground light must usually be around 3.2 by Weston exposure meter, south light 25-50, and overhead sky light (through the insectary roof), 25-100; however ground light may be as little as 1.6 and sometimes registers more than 6.5 before the first flights are made. A single butterfly once flew, at 5:45 A.M. in late April at a temperature of 73° F. (22.3° C.) when the ground light registered only .4, the south light 3.2 and the sky between 3.2 and 6.5. For comparison, noon conditions on a bright sunny day with a typical rainforest combination of some clear sky and some clouds show the following readings inside the insectary: ground 25-50, south 200, overhead sky 800. Full morning activity by all healthy individuals is reached when the temperature is at least 73° F. (22.3° C.) and the ground at least 13 Weston in some areas, south light 50 and overhead sky more than 50. Activity is always higher on sunny days.

The butterflies become inactive in rainy, dull or windy weather. They also often become inactive up to an hour before a heavy squall, even while the weather remains calm and bright. An attempt to link this with barometric pressure failed. On hot, dry afternoons the butterflies tend to fly high and erratically when the humidity drops below fifty per cent., batting against the roof and becoming exhausted. Sprinkling the insectary at once corrects this condition.

In bad weather, roosting—that is, hanging upside down from a twig or tendril, with the wings closed—may begin as early as 2:30 in the afternoon. On bright or moderately cloudy days, however, the first butterflies may start gathering in the roosting place around 4:45 P.M. in the average month of April, while others are still feeding. The majority hang up around 6:00 P.M. and all are in their final positions at 6:15. The time varies only about twenty minutes one way or the other from these hours on the longer and shorter days around the solstices. The temperature records during the going-to-roost period have ranged from 80° F. (26.7° C.) down to 73° F. (22.8° C.), and, as was said above, did not apparently affect the roosting behavior, which was primarily controlled by the decreasing light. When the ground-vegetation light recorded between 6.5 and 13 Weston, with the south over 25 and the sky overhead more than 50, nearly all the butterflies continued to feed, and courting sometimes took place. At intensities less than the above, the butterflies gradually gathered to roost. In one instance, an individual fed accurately and subsequently found the roost at the extremely low intensities of ground-vegetation .4, south 3.2-6.5 and sky 13. Feeding with a ground reflectance of 1.6, south 6.5-13 and sky 13-25 was not uncommon. It will be seen that these intensities are slightly lower than those at which the first morning activity usually occurs, when the tempertuare is nearly always lower than the low of 73° F. (22.8° C.) recorded for going to roost.

The conditions controlling first morning activity and roosting are summarized in Table 3. Although observations on other species are incomplete, it may be said here that forest-living ithomiids are active at both lower light intensities and lower temperatures, while *Heliconius sara* and *H. ricini,* which fly in slightly more open areas than *H. erato,* require either more light or higher temperature or both for activity. These characteristics lead, in the insectaries, to the ithomiids flying both earlier in the morning and later in the afternoon than *erato,* while *sara* and *ricini* both usually leave the roost later and hang up on it earlier than does *erato.*

D. Feeding. *H. erato* is altogether a flower feeder, never coming to fruit. From observations on feeding preferences in the insectaries, garden and in the field, Table 4 was compiled. *Lantana* has been observed to be strongly attractive in the field in both Venezuela and Surinam, as well as in Trinidad, and is far and away the favorite in the insectaries, being used as the staple diet.

Table 3. Relationship of Diurnal Activity to Temperature and Light in *Heliconius erato hydara*

Based on observations made in Trinidad, B.W.I., between December and June, altitude 800 feet. All light readings made under wire netting roof of insectary, with Weston photometer pointing directly overhead. For fuller data, see text.

	Morning (First activity: 5:45-8:00 AM) Light always more than 25 Weston			Afternoon (Last activity: 4:30-6:00 PM) Temperature always more than 73°F.		
Activity	Temp. < 67° F.	Temp. 67°-72° F.	Temp. > 73° F.	Light > 100 W.	Light 25-100 W.	Light < 13
Full	–	–	X	X	–	–
Slight	–	X	–	–	X	–
None	X	–	–	–	–	X

Feeding takes place all during the day, but is especially active on bright mornings between 9 and 11 A.M. When left undisturbed in the insectaries, neither sex seeks food until 20 to 24 hours after emergence; however, when presented with food some individuals will uncoil the proboscis and feed about six hours after emergence.

E. Social Behavior. Social behavior may be divided into three categories, namely, courtship, social chasing and roosting. The following paragraphs are descriptive statements; the activities will be analyzed in subsequent sections (p. 183 ff.).

1. *Courtship.* In the normal sequence, two alternative beginnings are possible. First, a male gives chase to a passing receptive female and pursues her closely. She usually settles on a fairly broad green leaf within a few moments, sometimes apparently urged to alight by the male's flying slightly above her and by actually brushing her wings with his on the downbeats, thus forcing her downward. Alternatively, a male approaches a female at rest on a leaf; her wings may be open or closed. Females which have already been stimulated by unconsummated courtships often will remain on the same leaf for hours, responding promptly to subsequent males.

At the male's approach, the female usually opens and closes the wings slowly several times. If she is receptive and begins to court, however, both pairs are held closed over the back. The male begins (Plate I, Figs. 1-3) by flying in short, repeated spurts close behind her, hovering in place, his forewings sometimes almost touching her hindwings and creating a current of air against them. Occasionally on a downbeat the male wings actually cover those of the female (Plate I, Fig. 4). During this stage, as well as in any preliminary chasing of the female, his fore- and hindwings are not separated to expose the silvery friction surfaces which apparently distribute the products of the scent scales (see p. 181). The male harpes are not in evidence, the tip of the abdomen remaining tightly closed, and no odor is detectable in this sex at this stage to the human observer.

The response of a receptive female to this buffeting is shown in two ways: first the abdomen is elevated and a gland, bright chrome yellow in hue, is extruded dorsally at the junction between the penultimate and distal segments. Two bulbous excrescenses project from it, one on each side of the dorsal midline, and are arhythmically inflated and partially deflated with waxing and waning stimulation. Below and behind them is the pair of tiny "stink clubs," described, along with the gland, in other heliconines by Müller (1877, 1912), and in this species by Eltringham (1925). These clubs are extremely difficult to see, even with a hand-lens, in the actively courting butterfly, and, indeed, are not exserted except during maximum excitement; however they are unmistakably in evidence in some frames of our motion pictures of courting females. The clubs show up as yellowish brown, in contrast to the chrome yellow of the gland proper.

Usually no odor is detectable to the human observer during this response of the female; rarely a musky odor is evident at very close range in individuals less than about two days old. Apparently this is the same odor which is detected when females are allowed to emerge from the chrysalid in a closed box; young males have, to human nostrils, a similar odor. Only in females which have been already mated and are being persistently courted on the following day, or, rarely, in which advanced courtship is disturbed so that the insects fly off with the female gland exserted, is a witch-hazel-like odor discernible during courting. This odor, well-known in the species, has no apparent effect on the courting male. (cf. "Defense," p. 180). Ford (1945, p. 96) has remarked that, unlike the products of male scent scales, the chemical attractants of female butterflies have not been reported as perceptible to human observers. Except for the circumstances just noted, this is true also of *H. erato*.

As the tip of the abdomen is elevated and the gland exserted, the anterior margins of the forewings, as they are held closed above the back, are pressed closely together. The more posterior portions of the forewings are allowed to bell outward. Simultaneously the hindwings are partly opened and rapidly vibrated for a second or two with brief intervals between vibrations.

The next stage of courtship, Stage II, may be omitted or strongly curtailed by excited butterflies when the female is highly receptive. Nevertheless, it is usually both well-marked and characteristic. The male shifts position from the rear forward, so that his flapping continues above her and, especially, immediately in front of her. He continues to face in the same direction as the female, or sideways, and he may or may not at times touch her forewings with the tips of his hindwings. His fore- and hindwings are now separated, sometimes widely, exposing the silvery friction surfaces (Plate I, Fig. 5; Plate II, Fig. 11). Both fore- and hindwings are in rapid motion (Plate II, Fig. 12), unlike normal flight, where the hindwings are almost motionless. A flowery fragrance can rarely be detected by the observer at this stage, probably emanating from the now-exposed friction surfaces. The tip of the male abdomen is still tightly closed. When both sexes are subsequently examined, both fore- and hindwings, especially near the bases and along the anterior margins of the hindwings, as well as the thorax, are found to be similarly fragrant. The female fragrance develops even in uncourted individuals, although to a lesser extent, and hence must be a product on her own, rather than merely sprayed on by the male in Stage II (see p. 182).

TABLE 4. FEEDING PREFERENCES OF *Heliconius erato hydara* IN TRINIDAD.

(Representative examples of both wild and garden species are included. Colors are roughly indicated of entire inflorescence, including bracts or rays, to give an idea of their variety. None of the whites and very few of these colors reflect more than minute amounts of ultraviolet. The important roles played by form and odor in the relative attractiveness of the different species are not considered here.)

	FREQUENTLY VISITED	
Loganiaceae.	*Buddleia variabilis* Faranchet.	Buddleia. Purple.
Verbenaceae.	*Lantana camara* L.	Lantana. Yellow & orange.
	Verbena spp.	Vervain. Purple; white.
Rubiaceae.	*Cephaelis tomentosa* Willd.	Wild Ipecancuanha. Yellow & red.
	Warszewiczia coccinea. (Wahl) Kl.	Wild Poinsettia. Yellow & red.
	Hamelia erecta Jacq.	Wildclove. Orange.
Boraginaceae.	*Cordia cyclindrostachya*. R. & S.	Black sage. White.
Compositae.	*Bidens pilosa* L.	Spanish Needles. Yellow & white.
	Senecio confusus Britten.	Gem of the Rio Grande. Orange.
	OCCASIONALLY VISITED	
Zingiberaceae.	*Costus spiralis* Rosc.	Scarlet Cane Reed. Yellow & red.
Orchidaceae.	*Epidendron fragrans* Swartz.	Purple Streak Orchid. White with purple streaks.
	Oncidium luridum Lindl.	Brown Bee orchid. Yellow & brown.
Asclepiadaceae.	*Asclepias curassavica* L.	Milkweed. Yellow & orange.
Solenaceae.	*Browallia americana* L.	False violet. Yellow & violet.
Gesneraceae.	*Tussacia pulchella* Rchb.	Harlequin Flower. Yellow, orange & purple.
Cucurbitaceae.	*Momordica charantia* L.	Carilla. Yellow.
	RARELY VISITED	
Musaceae.	*Heliconia hirsuta* L.	Paradise flower. Yellow & orange.
	Heliconia humilis Jacq.	Swamp balisier. Yellow & orange.
Bignoniaceae.	*Tabebuia serratifolia* (Vahl).	Poui. Yellow.
Rubiaceae.	*Ixora coccinea* L.	Ixora. Red.
	APPARENTLY NEVER VISITED	
Papilionatae.	*Erythrina micropteryx* Poepp.	Mountain immortelle. Orange-red.
Convolvulaceae.	*Convolvulus* spp.	Morning glory. Blue; yellow; white.
Bignoniaceae.	*Tabebuia pentaphylla* Hemsl.	Poui. Pink.
Malvaceae.	*Hibiscus* spp.	Red; pink; orange; yellow; white.
Plumbaginaceae.	*Plumago capensis* L.	Plumbago. Blue.
Campanulaceae.	*Centropogon surinamensis* (L.)	Presl. Crepe Coq. Red.
Acanthaceae.	*Pachystachys coccinea* Ns.	Black Stick. Red.

During Stage II the female continues to vibrate the hindwings while the anterior margins of her forewings remain closely apposed. When Stage II is prolonged, however, in its extreme form where the male fans her from a position in front of her, rather than directly above, she withdraws the abdominal scent gland and partly lowers the abdomen. Her antennae are occasionally lowered during Stage II, again principally when the male is courting from in front of her.

The final sequence, Stage III, immediately precedes copulation. It begins with the male's alighting and moving backward beside the female, on either side, but more frequently on the right. He still faces in the same direction as she, and he usually comes to rest with his eyes near the level of her thorax. He continues flapping his wings with the friction surfaces exposed and she once more elevates the abdomen and extrudes the scent gland. Fragrance is most likely to be detected at this stage, but its source cannot be determined because of the insects' activity. If Stage II has been omitted, the male simply alights beside her, his friction surfaces now being exposed for the first time. In any case he extrudes the harpes, twists his abdomen sideways, and seeks to curve it forward between the posterior margins of the female's now folded hindwings until the harpes can engage the female's abdomen. In fully receptive females the abdomen is by now lowered, the scent gland being simultaneously withdrawn. The harpes grasp the abdomen's lower tip, gripping it by the latero-ventral portion of the penultimate segment.

During copulation, which usually continues more than an hour and rarely overnight, both pairs of wings in both sexes are normally closed and held erect over the body in typical daytime rest position. The male swings promptly around so as to face in the opposite direction from the female. When disturbed a short flight is made to another resting place, the male carrying the inert female. No odor is apparent during copulation except for an occasional faint fragrance when, if slightly disturbed, the male slowly waves his wings.

Persistently courting males which are not accepted by females, or old males which have made repeated unsuccessful attempts to engage the female's abdomen, or males which have been courting females of another species (namely, *Heliconius melpomene, H. ricini, H. isabella,* and *Dryas julia*) sometimes come to rest in front of the female, facing her, which is a position atypical for this species. Alternatively, they may sit quietly beside her, their heads on a level with the female's head, or, more often, her thorax. From either position the male sometimes palpates the female's head, antennae or thorax with his antennae, and, rarely, with his uncoiled proboscis (Plate III, Figs. 13, 14). Another type of atypical behavior often occurs among the old males, which court facing the female, and flying both in front of, above and behind her, in irregular alternation; the males' friction surfaces remain exposed regardless of their position. None of the atypical behavior described in this paragraph occurs in the course of a normal courtship. It appears exceedingly likely that displacement behavior is involved, particularly when the proboscis is inappropriately extruded.

Courting may take place at any time during the day but is especially common during the late morning and after 2:30 P.M. Males almost never court females engaged in feeding at bunches of flowers, although they are not similarly restricted if the female is on an isolated blossom. There is no courting on the roost (see below).

Sometimes a receptive female which has not been courted will flutter the hindwings at the close passing of almost any species of butterfly; if she is more than two days old and still unmated, she may freely chase passing *H. erato* of any age; younger females, however, fly and feed very little.

Males and females both can mate at least twice, the males from the second to at least the thirty-first day after emergence. Some individuals court persistently but unsuccessfully for another month. Females have been seen mating from 45 minutes after emergence through the seventh day. The hindwing flutter and extrusion of the scent gland in response to courting takes place through the eighth day. However, the anterior forewing margins are held less and less tightly together following the third day, and the abdominal gland is extruded less and less completely.

2. *Social Chasing.* Chasing-and-circling, which seems not to be directly of a sexual nature, is a frequent activity of healthy male butterflies throughout their lives and of females which have completed egg-laying. The males and old females chase both one another and non-receptive females indiscriminately in short flights, sometimes with mutual circlings. Young males and newcomers to the insectary are especially subject to chasing. There is no apparent attempt to force a chased butterfly to alight, as in preliminary courtship, and the roles of chaser and chased are frequently reversed several times during a flight. The abdominal gland of the female is not exserted, nor are the male harpes, the friction surfaces are not exposed and there is no detectable odor of any kind. The flights are never the result of two or more males courting a single female, although this multiple courting often takes place. The chasings and circlings invariably end quite simply with the two or three butterflies involved going their separate ways.

Sometimes a butterfly will approach a resting individual, which is not a receptive female, from the rear, as in the first stage of courtship. The resting butterfly then opens and closes the wings slowly a few times, whether they have been held open or shut, whereupon the approaching individual flies away.

Except for the apparently non-courtship relationships described above, no approach has been found to inter-male threat display or fighting, nor is there evidence in the insectaries of territoriality or of a dominance order. Males and old females are far more active in both chasing and feeding than females which have not completed egg-laying.

3. *Roosting.* During the late afternoon *H. erato* follows the family habit of gathering in groups for the night. In the insectaries as in the field the butterflies often crowd the same dead twigs or vine tendrils, night after night, hanging upsidedown, the wings closed. Species of the same genus may roost with them. In the insectaries males and old females tend more to occupy crowded roosts together, while younger females, except when at their most receptive (the second through the fourth days), show less gregariousness. However, these receptive females usually roost on the more crowded perches, or sometimes next to a somewhat isolated male. No courtship takes place on or near the roosts, although there is always a great deal of activity, buffetting and pushing and jockeying for position, as the butterflies gather.

F. **Defense.** No organized work on the distastefulness of *H. erato* has yet been undertaken in the course of the present study. However, many casual tests have been conducted in our laboratories, both at Rancho Grande, Venezuela, and in Trinidad. Almost all of these confirm the heliconiid reputation of distastefulness to their natural predators. Butterflies of both sexes and all ages have been refused by various individuals of the lizard, *Polychrus marmoratus.* Some were seized by the wings or body and dropped, while others were disregarded altogether. In some butterflies the scarlet band was cut off by the observer before the insect was offered to the lizard. Individuals were also refused by the frog, *Hyla maxima.* Usually, but not always, they were refused, or examined and dropped, by captive capuchin monkeys. The butterflies were always either dropped or disregarded by the mantids *Stagmatoptera septentrionalis, Stagmomantis carolina* and *Oxyopsis rubicunda.* All of these laboratory test animals, from lizards to mantids, freely ate Lepidoptera of unprotected families and comparable size following the refusal of *Heliconius erato.* Ponerine ants, however, attacked and ate ailing *Heliconius* in the insectaries, and various non-ponerines scavenged them freely. Also, several species of epeirid spiders were major insectary enemies.

In *H. erato* three or four different odors may be distinguished by the human observer. All of them probably play roles in the insect's sexual or social patterns or in both. At least two of them and possibly all appear to be concerned also in the butterfly's defense. These odors and their sources will now be considered in turn.

1. *Abdominal Glands.* It has been generally held in the literature (see ref., p. 169) that the glands of the penultimate abdominal segment in the female, and in each harpe of the male are aposematic in function, discouraging attack by emitting an unpleasant odor. The scent has been variously compared with that of carbylamine, phenyl carbylamine, witch hazel, cashew oil from the shells, and, when less strong after a lapse of time, sweet briar. Some have considered the smell to be exceedingly unpleasant, others pleasant. However, as Eltringham (1925) pointed out, an odor which seems agreeable to one person may be obnoxious to another. For example, he himself did not like the scent of witch hazel, which is rated either "pleasant" or "not unpleasant" by all five of the present members of the Tropical Research staff.

The following account of the abdominal glands is derived from our Trinidad studies.

In *H. erato hydara* these glands in both sexes sometimes give off a strong odor which is practically never discernible in the course of courtship, and never at the roost or in social chasing. To us it always resembles witch hazel in the living or freshly dead insect. As noted by previous observers of this and other subspecies (Longfield, 1926; Collenette, 1929), the odor is stronger and occurs more frequently in females than in males. In the Trinidad form it appears in the female only after mating; it can be detected as a faint fragrance, similar to that of the wings (see below), almost immediately after copulation. It then develops slowly, becoming strongest in the midst of the oviposition period, then declines and has not been detected after the thirtieth day of the imaginal period. It does not deter either subsequent courtings or at least one additional mating. It never develops in unmated females, even after death; however, it may be strong in the glands, excised and bottled, of males and mated females for many weeks although, as will be discussed below, it alters its witch-hazel-like characteristics. The odor can only rarely be detected in living males of any age; those which emit the odor in response to seizures are usually moderately but not extremely young.

The abdominal glands are everted in apparent defense only when the insect is seized either near the base of the wings, or by the head, thorax or abdomen. The seizure may be by any means, whether a natural enemy, fingers or forceps. Grasping the tips of the appendages, or simply touching or tapping any part of the insect, does not evoke the response. Neither does a purely visual stimulus, or the odor of a lizard's cage. Also, as previously stated, it is a rather uncommon response, being fairly predictable only in moderately young, mated females, or when the abdomens of either sex are squeezed so forcibly that the extrusion may be considered a purely mechanical effect. It is only with the stronger stimuli that the "stink clubs" (p. 177) are exserted.

On the other hand, the ventral curving of the abdomen, which always accompanies extrusion of the gland, occurs to a greater or lesser extent, and without extrusion, whenever the insect is seized as described above. It will be noted that this abdominal curving-under is in the opposite direction from the upward tilting of the female abdomen when the gland is everted during courtship (p. 177). The restricted use of the gland in defense is true of field-caught as well as insectary-reared specimens, although it may be that male responses are even rarer in these "tame" butterflies. However, insectary females of appropriate age respond fully to seizure, and evert the glands even late in life, when no odor can be detected.

Dr. Eltringham's (1925, 1926) dissections and serial sections of the abdominal glands in the female of this species and subspecies showed only a single pair of glands, although there were two pairs in related genera. It seems likely therefore that the protective function, if any, of the strong odors evolved directly out of the sexual function, and that their chemical composition is not necessarily different from the substance(s) obviously used in courtship but not detectable to the human sense of smell. The actual courting use of the glands in the female, apparently reported for the first time in the present study, confirms Eltringham's surmise concerning such a function in addition to that of defense.

In comparison with *H. besckei* in Brazil (Müller, 1877, 1912), *H. erato* has this defense mechanism much less well developed. It may be that *H. erato* represents a preliminary stage in evolution, in which the everting of the glands when the insect is prevented from escape, and the concomitant discharge of abundant odoriferous material, is scarcely more than displacement behavior in which a sexual response is given. In other species of the group it has probably developed into a highly evolved defense. According to Müller it was a habitual defense response with both sexes.

Mr. Ernest C. Crocker of the Flavor Laboratory of Arthur D. Little, Inc., in Cambridge, Mass., has most kindly given his impressions on samples sent him of the harpes of a 72-hour-old male and the abdominal scent gland of a 16-hour-old, mated female. Mr. Crocker and two assistants examined the material within five to six days after the specimens were killed and sent to him in small vials, via airmail. He writes as follows (personal communication): "The . . . . *Heliconius erato* specimens are all animal-like, earthy, musty, and dulcy, and yet somewhat flowery. Their distinctive features follow . . .

"The harpes, 72 hours old, have distinctly phenyl carbylamine character (see next description).

"The scent glands ♀, 16 hours old, have particularly sharp, strong phenylcarbylamine (phenyl isocyanide, $C_6H_5\text{—N=C}$ type) odor. This odor also suggests styrene (phenyl ethylene) and phenyl proprionaldehyde. Enclosed is some of that aldehyde and also some brom-styrene. In our opinion, this insect odor must be due to a phenyl compound, with no more than 2 or 3 carbons on the side chain and possibly an oxygen or nitrogen."

The odors of the samples, when compared with living specimens in Trinidad, did not bear any obvious similarity to those of the abdominal glands of either sex; however, within a few days the odor of the excised glands decidedly resembled the brom-styrene sample.

2. *Scent Scales.* As in other species of the genus (Müller, *loc. cit.*), specialized scent scales are present in the male only, and only on the friction surface of the anterior portion of the

upper hindwing. In the present species they are small, dark, and mostly concealed by the larger uncolored scales of the friction surface. Although they apparently play a definite role in courtship (p. 179), their odor is only rarely and questionably detectable in courting males. In fresh or long-preserved friction surfaces, however, the odor is moderately strong, and to us appears decidedly flowerlike. Mr. Crocker examined samples of this area, from the 72-hour-old male mentioned above, and noted that the general character was that of the abdominal glands, namely "animal-like, earthy, musty and dulcy, and yet somewhat flowery." In distinctive features they were "tobacco-like, somewhat fecal (scatole) and have some finnanhaddick amine character. No carbylamine-like odor noted."

3. *Odor of Thorax and Wings.* A fragrance, apparently distinguished here for the first time, is clearly perceptible in both sexes on the dorsal side of the thorax and on the upper surfaces of all the wings, especially basally. To our perception it is not distinct from the fragrance of the scent scales proper, except that it is weaker. In dried specimens or detached wings, even many weeks after death, there may be, as in the abdominal glands, a resemblance to the odor of brom-styrene. In living butterflies this fragrance does not become apparent until about the second day in females and the third in males. The odor does not depend on mating or even courting to be evident in females; therefore at least in these females it cannot be merely the result of fanning the products of the scent scales by courting males.

4. *Odor of Young Imagos.* A musky odor is evident in very young imagos; usually it is not detectable after about the third day. It has not been definitely localized except that rarely it has seemed strongest at the tip of the female abdomen.

To summarize: Three or four distinct odors are discernible to human beings in *H. erato;* at least two of them are probably involved in defense. First, the abdominal glands emit an odor which, in the intensity detectable to human beings, is at least indirectly a product of the male harpes; it reaches its maximum development in mated females. It is a phenyl compound which changes, for human sense, from a witch-hazel-like to a phenyl-carbylamine-type odor within a few days. The odor which almost certainly is emitted by the extruded gland of unmated females during courtship is not detectable by the human sense of smell. Second, as in other members of the genus, fragrant scent scales are present on the anterior upper portion of the male hindwing. Third, a fragrance, apparently similar both to that of the male scales and, faintly, to that of the abdominal glands, develops on the thorax and upper wing surfaces of both sexes, mated and unmated. Fourth, a musky odor is apparent only in recently emerged imagos, especially females, and is possibly strongest at the distal end of the abdomen.

Any defensive use of the witch-hazel-like odor of the abdominal glands seems to be quite obviously a secondary development from an originally sexual function. A puzzling point is that the odor reaches maximum strength in ovigerous females. Since these are biologically the most valuable members of the species, it is possible that their increased odor has indeed some selective significance. However individuals of this age do not seem to be more resolutely refused by predators than are others of the species.

It seems that the basis of the aposematic taste of these butterflies may very likely be a secretion of the thorax, or of the thorax and the wing bases, which may be also responsible for the fragrance of these regions in both sexes. Perhaps it is contained in the weather-proof oily coating of the scales. The odor probably also has a sexual, or at least a social significance within the species.

The function of the male scent scales is probably sexual only. The musky odor of young adults may well be of value both socially, sexually and aposematically.

An interesting related question is that of the general function of odor as an aposematic signal in various Lepidoptera. Some authors have remarked both on this protection and, simultaneously, on the avian beak marks which often show on the wings of living butterflies, and so indicate successful past escapes. Assuredly birds must be the chief natural enemy of adult diurnal Lepidoptera. Yet these vertebrates, according to the best current knowledge, cannot smell. The chemical source of the nauseous taste must therefore extend to the insects' wings' themselves, being perhaps contained, as suggested above, in the oily scale coating. The odor(s) of the insect, as opposed to the taste, must be chiefly of use in deterring reptilian and mammalian enemies.

It also seems clear, as suggested by Jones (1930, 1931), to anyone who has observed sleeping heliconiids in the field, that the protection afforded by roosting aggregations is that of reinforced odor rather than of conspicuous warning color. Roosting heliconiids, of whatever species, are exceedingly inconspicuous objects even in daylight.

G. Oviposition. The foodplant of *H. erato hydara* in Trinidad is *Passiflora tuberosa* (Jacquin). Eggs are laid only on the youngest shoots and tendrils, generally one to a plant. The vines seldom grow taller than six feet, each shoot dying back after flowering and the young shoots tending to come from the ground or near it. Hence laying females usually fly only a few inches or several feet above the ground. Most eggs are laid between noon and 2:30 PM, which is otherwise a period of relative quiescence for the species. One egg, however, was laid at 8:45 in the morning and another as late as 3:30 PM. The first egg normally appears on the eleventh or twelfth day after emergence, although a single individual, mated with a Surinam male 45 minutes after emergence, laid the first egg on the fourth day; another female commenced laying on the tenth. In no other females, among more than 20 recorded layers of known age, was an egg laid earlier than the eleventh day. Egg-laying continues at the rate of 0 to 4 eggs, very rarely 6, daily for about two weeks or slightly more, until a total of up to about 24 eggs have been deposited. A typical female laid 18 eggs in 15 days, with a final gap of four days between the seventeenth and eighteenth egg. The higher numbers, two to four a day, are laid in the first half of the period.

H. Longevity. Under ideal conditions, males usually live in the insectaries slightly more than a month after emergence although rare individuals live more than two months. Females habitually live six weeks or more, again if no untoward circumstances, such as long rainy or windy spells, occur. The record for any individual was 91 days in the imaginal state, attained by a female reared in captivity. She had been mated on her third day and laid about 20 eggs on schedule. Counting the total 26 to 30 days of the developmental stages, this gives a record lifespan of about four months.

VI. Experimental Analysis of Social Behavior

A. Introduction. Experimental work was undertaken in order to determine the releasing mechanisms of courtship and other types of social behavior. In particular it was desired to discover whether any role was played by color in these activities, and if so, whether it was as an innate or acquired response.

The evidence was accumulated in three ways: first, through concealing the female so that only her odor could guide the male, the sense of sight being altogether or partially eliminated. Second, the color and pattern of both sexes were changed in various ways, in order to establish the relative importance, if any, of hue, brightness and markings. Third, the responses of both sexes were tested with models.

B. Work with Concealed Females. 1. *Method.* Six virgin females, each between 24 and 72 hours after emergence, were placed, singly, in a box 2 × 2 inches in size, which gave them sufficient space in which to move their wings freely. In the first tests the cardboard covering top and bottom was punctured with about a dozen nailholes, through which the female was quite invisible; in other tests the top was covered with khaki-colored mosquito netting, which presumably made the odor of the female more discernible, but through which she was dimly visible to the human observer. Each of the butterflies, before being placed in the box, had been tested with one or more young males and found to be normally attractive—that is, she elicited Stage I courting behavior.

2. *Results.* When the box with an enclosed female was left on a stool in the insectary, in the path of freely flying males, none ever dipped toward it, or paid it any other evidence of attention, whether the box was covered with punctured cardboard or netting. Similarly, virgin females kept in a cage 18 × 18 × 12 inches, with one of the long sides covered with wire netting, did not attract the attention of males. It is concluded that female odor alone is not sufficient in this species to inaugurate courtship.

C. Work with Painted Butterflies. 1. *Method.* A variety of unsuccessful preliminary attempts was made to change the color of a living butterfly. Sometimes the color, such as water color or India ink, would not adhere to the oily surface of the scales. Removal of the film with weak acid damaged the wing, as did bleaches strong enough to fade out the black pigment. Painted tissue attached to the wing with an appropriate cement was so heavy that the butterfly could not fly. Certain paints, such as artists' oils, did not dry fast enough. Finally, the butterfly was often so badly shocked by the procedure—apparently because of the necessary handling—that it never recovered normal activity levels and died more or less promptly.

The following technique, however, was slowly perfected and can now be recommended (Pl. III, Fig. 15). The main precautions to be observed are to work slowly and to touch the butterflies with the fingers as little as possible. Properly done, no manual handling whatever is necessary, after the butterfly has been placed in the envelope, and hardly any touching with forceps. Stroking with the paint brush should be feather-light.

Step. 1. The butterfly is placed in a glassine envelope, the wings folded over the back, as soon as captured, either in the field or the insectary; handling and warming are avoided. With specimens taken from the insectary, capture and painting is done with the least shock at night, the insect being taken from the roost. After painting it can frequently be rehung in approximately the same place.

Step 2. The envelope is placed in a flat wooden box about 3 × 3 × 1 inches, with a glass bottom. The box is turned upside down so that the butterfly can be observed through the glass. Through one side of the box enters the nozzle of a short tube attached at the other end to a small fire extinguisher or bicycle pump filled with carbon dioxide. The stopcock of the cylinder has previously been turned on and the gas regulated to a very low rate of flow. The butterfly in the envelope is left in the box for three to five minutes, or until a minute or two after all movement has stopped. If the butterfly becomes active during painting, it can be further anaesthetized merely by placing the glass-bottomed box briefly over the insect on the spreading board (see below). Deep anaesthetization should be avoided, since butterflies so treated do not always regain their normal vigor, and may not court.

Step. 3. A piece of oiled paper is laid across the slot and breadth of the butterfly spreading board, to support the body in a sling and protect the wings from the wood. The butterfly is shaken onto the paper and, with the wings remaining folded, fastened into place with two strips of paper pinned across, but not through the wings, in such a way that the area of underwing to be painted remains uncoverd.

Step 4. With a fine paint brush ether is brushed lightly several times across the area to be painted.

Step 5. The underwings of one side are painted as desired with a waterproof, fast-drying lacquer. In the present experiments, "Flopaque" was used (manufactured by Floquil Products, Inc., Cobleskill, New York). The paint should be applied thinly and restroking avoided.

Step 6. Papers are removed, the butterfly flipped over, and the underwings of the other side similarly treated.

Step 7. By careful manipulation of paper strips, the butterfly's wings are now opened and fastened to the board, without the touch of fingers or forceps. Extreme care must be used not to exert pressure on head or body by pinning their paper covering too tightly or by letting the wax paper sling under the body become taut. A strip loosely covering eyes and body, however, helps keep the insect quiet when it starts to emerge from the anaesthetic. Brushing with ether and painting then proceeds as on the underwings.

Step 8. After painting is completed the setting board is taken to the insectary and the butterfly released by unpinning the paper strips, thus avoiding further handling. When the procedure is properly carried out, the insect is usually capable of flying at once to a resting place. When the painting has been done at night, the butterfly can often be simply rehung with forceps on the roost. In any case, the butterfly usually remains quiescent for some hours, although females give normal courting responses sooner. Recovery should be altogether complete by the next day. When possible, butterflies should not be painted sooner than 48 hours out of the chrysalid, since the wings of freshly emerged butterflies are very easily damaged and the insect is more subject to aftereffects of the treatment. However, for special procedures employed to ensure a butterfly's being unconditioned to the color "red," see p. 187.

If the use of other types of paints is desirable, such as fluorescent paints, or water colors with particular spectral characteristics, they may sometimes be successfully applied as follows: the coloring matter is painted on a sheet of lens tissue and allowed to dry, in several coats if necessary, so that the tissue becomes opaque. The paper is then cut in pieces of the desired size and shape. The butterfly is anaesthetized and placed on the spreading board as for painting. The painted bits of tissue are fastened in place with rubber cement diluted with xylene. The method is only rarely satisfactory, since the extra weight often prevents the butterfly from flying well. No successful attempts have been made to remove the insects' scales before attaching the paper, and so reducing the weight of paint needed to efface the natural color; the wing tissue is always too much weakened either by the use of chemicals or by stripping with Scotch tape.

Table 4 gives a summary of the various color and pattern changes effected; Table 1 (p. 172) shows a spectrophotometric analysis of the paints used.

No positive responses are included where there was danger of the female's showing effect of summation. The experiments were conducted both with individuals which had emerged and been kept in isolation, out of sight of their own species, and not allowed any sight of the color red, and those which had not been so isolated (see p. 187).

2. *Results.* In brief the following principles may be stated, concerning the social responses to painted butterflies.

a. *Courtship.* These responses are given in summary in Table 4. Positive responses were counted for the sex involved if the female, when approached or actively courted by a painted male, elevated the abdomen, extruded the yellow organs, apposed the forewings and vibrated the hindwings. If only the abdomen was elevated and the yellow organs extruded, a half-response was counted (the hindwings were never fluttered without the abdominal response). The very rudimentary response of merely raising the abdomen slightly, without extruding the yellow glands, was not counted, since this is sometimes done when the insect is resting alone, or feeding.

Positive responses were counted for males to painted females if he approached the female and made repeated, continuous courting dashes at her, in at least the typical Stage I rear position (p. 177).

It will be seen from Table 5 that all changes of color and pattern attempted resulted in positive responses in at least one sex. What cannot be fairly indicated in the table, because of the difficulties of the procedure and the many variables of weather, physiological state of the butterflies and so on, is the relative popularity of the various colors. This can be recorded only in general terms, resulting from the author's prolonged observation of painted butterflies over a three-season period. It was borne out in every respect in the amount of general social chasing of the variously painted individuals by other members of the group after the active breeding age was passed (p. 180).

Briefly, the farther the altered color of the forewing pattern is distant from the normal scarlet in the spectrum, the less notice is taken of the butterfly, either by the opposite sex or as a subject for general social chases. That is, butterflies with the forewing band painted orange or yellow were almost or quite as successful socially as butterflies repainted in natural colors. In most trials the orange was more successful than yellow, that is, more promptly responded to by members of the opposite sex, and slightly more subject to social chasing than yellow. Yellow-green bands were less successful, while greens, blues, violet, positively ultraviolet white and all black were least so. Negatively ultraviolet white was, again, moderately successful, but since for this color Chinese white (zinc oxide) water color on bits of tissue had to be used, the butterflies were both overburdened and scarcely weather-proof; hence their general social life when fitted with this color was not subject to valid comparisons.

All-black butterflies and those with inconspicuous short-wave markings, such as all black with dull green radiations on the hindwings, were notably unsuccessful. In fact no completely black female, with even the pinkish underband of the forewing eliminated, ever drew a positive response from a male; the one case of mating given in the table was a young female which had been given only a thin wash of black, permitting a pinkish tinge to show both above and below. Out of eight individuals painted more or less black, this was the only positive response. Black females were repeatedly ignored, even though, at the close passing of males, all the usual Stage I responses were given: apposed forewings, gland extruded from the elevated abdomen and vibrated hindwings. Occasionally these unnoticed females even chased after such passing males, yet never attracted more than the briefest dips in their direction.

b. *Social Chasing.* Behavior toward males and non-receptive females which had been painted, paralleled that of courting individuals. The farther away the spectral reflectance of the paint used from the orange-red region, the less was the butterfly chased. This was regardless of brightness: pale blues, greens or green yellows were disregarded in comparison with deep oranges and reds. Grays were treated like black. Often an ignored painted female would chase other butterflies, which even then would only rarely take any apparent notice of it. There was no reciprocal circling. Blue-marked butterflies, which often lived weeks after painting, were ignored almost or quite as completely as all-black individuals.

c. *Roosting.* In this activity the painting of individuals made no apparent difference. All were accepted on the roost, and made and held for themselves positions in close juxtaposition both to normal butterflies and to those otherwise colored.

D. WORK WITH BUTTERFLY MODELS. 1. *Method.* The most successful models were made of heavy black or colored cotton felt or canvas cut roughly to the shape and size of a *Heliconius erato.* To these were fasted bits of colored paper in various sizes and patterns. Along the longitudinal axis of the "body" of each model was threaded a black insect pin. The other essential part of the apparatus was a flexible 2½-foot wand of split bamboo. To the small end of the wand was attached a small magnet, such as is used for fastening notes to bulletin boards. A petroleum-base adhesive attached the magnet to the bamboo, both magnet and wand being painted dark green and black. By means of the magnet and the insect pin through the body of each model, a series of different models could be presented to a butterfly in as rapid succession as desired.

Table 5. Alterations Effected in Color of Living *Heliconius erato hydara.*

Each color change indicated by "X" was effected in at least one butterfly of each sex. The responding individual, painted or not, had not been allowed previously to see the color red, except that of its own wings. Positive courting responses, sometimes including copulation, were obtained at least once for each color change effected in each sex. However, responses were exceedingly rare, and almost always weak to the blues, greens and blacks, while oranges and yellows were treated almost like normally colored butterflies. Change in pattern was of relatively little importance. Females were in general less influenced by color change than were males. Numbers in parentheses after color names refer to paints used (For spectrophotometric analyses, see Table 1, p. 172).

		No Color Added	Red (31)	Orange (25)	Yellow (20)	Green (12)	Blue (5)	Blue-green (10)	White (UV Positive)	White (Zinc Oxide)	Pink (36)
Red forewing band unaltered	Hindwing with spot		X					X			
	Hindwind with radiations		X				X				
	Under fore- and/or hindwing with spots, crosses, dots, in many combinations (for identification)		X	X	X	X	X	X	X		
Forewing band altered in color (upper & underwings)	Hindwing unaltered			X	X	X	X	X	X	X	X
	Hindwing with spot of same color			X	X			X			
	Hindwing with radiations added				X						
Upper forewing band altered in color, blackened on underwing	Hindwing unaltered			X				X	X		
Upper forewing band blackened	Underforewing band painted								X		
	Underforewing band unaltered (pale pink, pos. UV)	X									
Forewing band blackened on upper & underwings	Hindwing unaltered	X									
	Forewing with colored spot, hindwind unaltered		X								
	Hindwing with spot				X				X		X
	Hindwing with radiations					X	X				
	Fore & hindwing with single spots				X						
Upper forewing band altered in color, underforewing band painted white (pos. UV)				X				X	X		

The most successful, and in general the only successful technique, consisted in jiggling the wand gently up and down near the butterfly to be tested by holding the wand in the left hand and tapping it rapidly near the base with the right forefinger. This caused the model at the tip to flutter up and down in a fairly realistic way. When models made entirely of paper had to be used (because of desired spectrophotometric characters), an underlayer of flapping black felt beneath the stiff paper gave the air current which is an important factor in the species' courtship pattern.

As in the work with paints, spectrophotometric reflectance curves were secured for the colored textiles and papers used (Table 1, p. 172).

The experiments were conducted in three groups. First, with individuals which had not been kept isolated, after their emergence, from normally colored members of their species, and which hence might have become conditioned to the color "red." Second, with individuals which had been kept in isolation from the time of their emergence until the hour of the experiments. These butterflies were not fed at all, or allowed to see any red object, even being isolated from other chrysalids, lest the red wing band which shows through the chrysalid on the last day before emergence should be seen by and possibly imprinted on an emerging neighbor. The isolated individual, after 24 to 48 hours, was then painted or not, depending on the needs of the subsequent experiment.

The isolation of unpainted examples was maintained as follows: The cages were kept at a distance from one another and from the insectaries, and the sides facing occupied cages were masked with branches. Wild *erato* almost never enter the garden where the small cages are kept, so there was very slight chance of conditioning by the brief sight of a passing member of the species.

The third group of test butterflies was even more rigidly guarded against possible conditioning to red. In this group the possibility was eliminated that a just-emerged butterfly might be conditioned or imprinted with the red color of its own wing markings, whether the scarlet forewing bands or even the tiny red dots and bar near the base of the underwings. It proved difficult to control this factor, but the following technique finally resulted in active, uninjured butterflies, fully protected against a previous sight of red, in about seventy-five per cent of the individuals treated.

Caterpillars of the imagos to be tested under these conditions were reared in complete isolation, as in the second group described above, and allowed to pupate hanging from a four-by-four inch piece of glass. On the night before emergence, the glass with its dangling chrysalid was placed over a hole in the lid of a light-tight shoebox. On top of the glass was placed a six-by-six-inch Corning Glass filter (Col. spec. 5-60, "H.R. Lantern Blue"); while transmitting the near-ultraviolet, violet and blue freely, it has a sharp cut-off in the green at 520 mμ. The filter was tightly sealed into place with black photo tape. Under this blue filter the test butterflies, in turn, emerged on schedule and were found on release to be less battered than those which emerged in complete darkness. Each individual, when examined the same evening under an identical blue filter fastened over an electric desk lamp, was found to be fully expanded with the wings relatively firm. The room was kept in complete darkness except for the blue light, so that the butterfly at no point had an opportunity to catch sight of its own scarlet markings. The butterfly was then removed from the box, anaesthetized with carbon dioxide and fastened on the spreading board, as in the usual painting technique (p. 183). The only difference was that after each wing surface had been arranged in position for painting, the eyes were covered closely with criss-crossed strips of black felt. This enabled actual painting to proceed under ordinary electric light, without the use of the blue filter. A blue paint, with relatively low reflectance in the long wave regions, was used (Sample 5, Table 1). After completion of the painting, the butterfly was hung in the insectary, from which all red or orange flowers had been removed, as well as all other butterflies. The young butterfly was allowed to feed well the following morning. Usually these butterflies which had emerged in a small box, been kept there all day and painted less than twelve hours after emergence were not in condition for testing until the day following feeding, that is, 48 hours after emergence. One did not become fully active until his seventh day, when he was successfully tested. The mortality is in any case high from this rough treatment, but the results, from the seven specimens which survived it, seem conclusively to be based on innate, and not learned or imprinted, behavior. These results (Table 6) agree extremely well with those obtained for the more numerous individuals tested in the other two groups, in which previous exposure to red was either partially or not at all controlled.

Throughout the experiments in all three groups, no positive responses were counted where there was danger of the female's showing summation, or heterogeneous summation. A model, normally unsuccessful, such as plain

TABLE 6. RESPONSES OF BLUE-PAINTED *H. erato hydara*, REARED IN ISOLATION, TO MODEL BUTTERFLIES

Part a: Field Data

Explanation: Each of the 7 specimens was maintained in isolation, without exposure to orange-red or red, until the time of the test. See text, p. 187 ff. All tests were conducted in calm, sunny weather in the large insectary. Each model (p. 185, Text-fig. 2, Pl. III, Fig. 17) was presented for a maximum of 30 seconds. A response, if any, usually occurred within five seconds. In males, a single slight dip toward the model was counted as a "minimum" response, several dips or short chases as "good," and definite Stage 1 courtship, with persistent pursuit, as "strong." The single female's responses were similarly gauged from the strength of her courting behavior, shown by the degree of abdomen elevation, extrusion of yellow gland, apposition of forewings and fluttering of hindwings. Color sample numbers refer to spectrophotometric analyses in Table 1, p. 172.

Individual No.	Presentation Order	Color Sample No.	Model Type	Model Hue	Response
1(♂)	1	4	2 colored bands on black	Blue	None
	2	8	“	Blue-green	None
	3	15	“	Yellow-green	None
	4	28	“	Orange-red	Good
	5	17	“	Yellow	None
	6	22	“	Yellow-orange	Minimum
	7	9	“	Blue-green	None
	8	33	Solid color	Red	Good
	9	—	“	Black	None
	10	23	2 colored bands on black	Orange	Good
2(♂)	1	4	2 colored bands on black	Blue	Minimum
	2	15	“	Yellow-green	None
	3	17	“	Yellow	Minimum
	4	8	“	Blue	Minimum
	5	28	“	Orange-red	Strong
	6	22	“	Yellow	Minimum
	7	33	Solid color	Red	Strong
	8	4	2 colored bands on black	Blue	Minimum
	9	23	“	Orange	Good
	10	8	“	Blue	None
	11	29	“	Red	Strong
3(♂)	1	7	Solid color	Blue	None
	2	14	“	Green	None
	3	18	“	Yellow	None
	4	27	“	Orange	Good
	5	7	“	Blue	None
	6	33	“	Red	Good
	7	36	“	Pink	Minimum
	8	22	“	Yellow	None
	9	33	“	Red	Strong
	10	4	2 colored bands on black	Blue	Minimum
	11	16	“	Green-yellow	None
	12	17	“	Yellow	None
	13	22	“	Yellow	Minimum
	14	8	“	Blue	Minimum
	15	15	“	Yellow-green	None
	16	23	“	Orange	Good
	17	16	“	+UV White	Minimum
	18	4+28	2 colored bands on color	Orange-red on blue	None
	19	28+22	Colored stripes on black (Text-fig. 2c)	Red; Yellow	Minimum
	20	—	2 colored bands on black	Zinc oxide white	None
	21	28	“	Orange-red	Strong
	22	16	“	Green-yellow	None
	23	34	“	Violet-red	Strong
4(♂)	1	7	Solid color	Blue	None
	2	11	“	Blue-green	Minimum
	3	18	“	Yellow	Minimum
	4	27	“	Orange	Strong
	5	7	“	Blue	None
	6	33	“	Red	Strong
	7	4	“	Blue	None
	8	17	“	Yellow	None
	9	22	“	Yellow	None
	10	28	“	Orange-red	Strong
	11	9	“	Blue-green	None
	12	36	“	Pink	Good
	13	17	Black stripes on color (Text-fig. 2d)	Yellow	None
	14	1	Solid color	Violet	None
	15	16	2 colored bands on black	Green-yellow	None
	16	34	“	Violet-red	Good
	17	—	“	Zinc oxide white	Minimum
	18	28	“	Orange-red	Good
5(♂)	1	7	Solid color	Blue	None
	2	18	“	Yellow	None
	3	27	“	Orange	Strong
	4	14	“	Green	None
	5	33	“	Red	Strong
	6	18	“	Yellow	None
	7	28	2 colored bands on black	Orange-red	Strong
	8	22	“	Yellow	None
	9	33	Solid color	Red	Strong
	10	23	2 colored bands on black	Orange	Strong
	11	22	“	Yellow	Good
	12	16	“	Green-yellow	Minimum
	13	8	“	Blue	None
	14	33	“	Red	Good
6(♂)	1	7	Solid color	Blue	Minimum
	2	14	“	Green	None
	3	18	“	Yellow	None
	4	27	“	Orange	Good
	5	7	“	Blue	None
	6	36	“	Pink	Minimum
	7	33	“	Red	Strong
	8	4	2 colored bands on black	Blue	None
	9	—	“	+UV White	None
	10	22	“	Yellow	Good
	11	17	“	Yellow	None
	12	29	“	Red	Good
	13	7+28	2 colored bands on color	Orange-red on blue	None
	14	28	2 colored bands on black	Orange-red	Strong
	15	34	“	Violet-red	Good
	16	16	“	Green-yellow	None
	17	23	“	Orange	Strong
	18	33	Solid color	Red	Strong
7(♀)	1	33	Solid color	Red	Strong
	2	27	“	Orange	Strong
	3	7	“	Blue	None
	4	14	“	Green	None
	5	18	“	Yellow	None
	6	36	“	Pink	Minimum
	7	7	“	Blue	None
	8	27	“	Orange	Good
	9	33	“	Red	Strong

TABLE 6. *(Continued)*

TABLE 6. *(Continued)*

10	22	2 colored bands on black	Yellow	Minimum
11	4	"	Blue	None
12	23	"	Orange	Minimum
13	17	"	Yellow	Minimum
14	–	"	Zinc Oxide White	Minimum
15	29	"	Red	Minimum
16	16	"	Yellow-green	Minimum
17	28	"	Orange-red	Good
18	33	Solid color	Red	Good
19	28+4	2 colored bands on color	Orange-red on blue	None
20	34	2 colored bands on black	Violet-red	Good

Part b: Summary

Color Sample No.	Hue	Responses*			
		None	Minimum	Good	Strong
–	+UV White	1	1	–	–
–	Zinc oxide White	1	2	–	–
1	Violet	1	–	–	–
4	Blue	4	3	–	–
7	Blue	8	1	–	–
8	Blue	3	2	–	–
9	Blue-green	2	–	–	–
11	Blue-green	–	1	–	–
14	Green	4	–	–	–
15	Yellow-green	3	–	–	–
16	Green-yellow	4	2	–	–
17	Yellow	4	2	–	–
18	Yellow	5	1	–	–
22	Yellow-orange	3	4	2	–
23	Orange	–	1	3	3
27	Orange	–	–	3	3
28	Orange-red**	–	–	3	5
29	Red	–	1	1	1
33	Red**	–	–	4	9
34	Violet-red	–	–	2	1
36	Violet-pink	–	3	2	–

*Black models with colored bands and solid colored models only.

**Used frequently, to check condition of specimen.

black felt or a stick, was used as a test in suspected cases. Contrariwise, a butterfly's threshold was gauged periodically during an experimental session by presenting a highly successful model. If a positive response was given to this, the insect was considered still to be in a mood adequate to continue the session.

In the entire series of tests, 53 young butterflies were used, including 30 males and 23 females. Of the total, 25 had not been isolated from their own species, 21 had been isolated from red except for the sight of their own scarlet wing band, and 7 were both isolated and painted blue.

2. *Results.* Since the factor of odor was removed, and movement controlled, the results were more clean-cut than in the case of painted specimens.

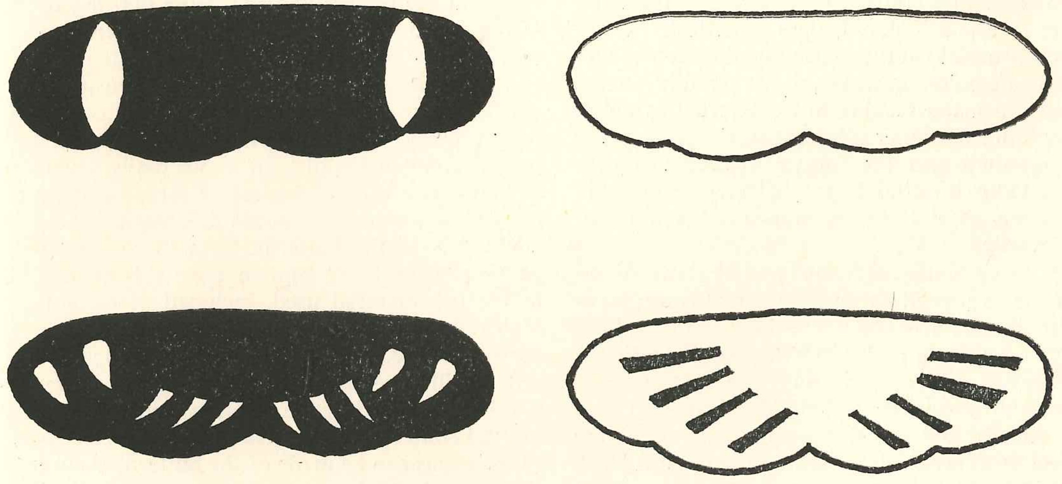
It was found through the use of models that both motion and hue are of importance in courtship. In order to elicit the hindwing flutter of females, the model had to be waggled up and down immediately behind, but not touching, her hindwings; the determining factor in this stage was the air current thus formed. A model, otherwise highly successful, which was vibrated to one side or in front of her, as in later stages of courtship, did not cause her either to raise the abdomen, extrude the yellow gland, appose the forewings or flutter the hindwings.

The response of males to models was partly to the fluttering movement of the model. Motionless models, tied by black threads to twigs or leaves, or left on the ground, only very rarely elicited a dip from a passing male. Models fluttered on the wand, however, were often chased and more rarely drew the first stage of courtship, that is, repeated short dashes with the friction surfaces not exposed.

The various models themselves were successful in direct proportion to their similarity to the size and color of living butterflies, with one exception; the most successful model of all was made entirely of negatively ultraviolet red felt without any pattern whatsoever; in fact it acted as a supernormal stimulus, eliciting a response from either sex when not only all other models failed, but often when the threshold was so high that a living member of the opposite sex in an appropriate physiological state did not win a response. It was accordingly used to test the continued responsiveness of an individual from time to time during a series of tests, or to determine its threshold before an experimental session.

Models with forewing bands of naturalistic size and position but varying only in color were successful in about the same sequence as were butterflies with the bands painted: the most successful were the naturalistic orange-red. However, the red, orange and yellow-orange were almost equally successful, lemon yellow and greenish yellow notably less so, while greens, blues, violets and positively ultraviolet white least so. In general, the colors reflecting ultraviolet the most strongly were less popular in comparison with purer colors of the same general spectral region. Negatively ultraviolet white drew responses rather unpredictably; on the whole they were moderately successful with individuals of low threshold. No response was obtained to an all-black model except weakly, by several females of very low threshold which were already highly stimulated by preceding models or by actual courting. These individuals responded equally well at that stage to practically any small object moved close behind them, including dead twigs and the observer's finger. Pattern was of little importance, so long as the background was black. Text-fig. 2 shows the type of variations used. However—except for the solid color red models, approaching the natural color of the butterfly's band—solid colors, with or without contrasting or gray bands or other markings, were less successful than their counterparts in which the model was black with a band of unnatural color. For example, an all-yellow model was less successful than a black model with a yellow band. An all-orange model however usually elicited a strong positive response.

Models with a wingspread of from about two-thirds to one and a half times normal were of acceptable size; models notably smaller or larger than these were unsuccessful, regardless of color or the individual's threshold.



TEXT-FIG. 2. Examples of models used in butterfly courtship experiments. **A**, normal type: black with colored bands; **B**, solid color; **C**, colored stripes on black; **D**, black stripes on color. Natural size.

Table 6 gives the series of responses by the seven individuals in which all chance of conditioning to red was avoided. Because of the importance of the order of model presentation the full field data are given in Part a. In the summary of the table, Part b, it will be seen that the results follow closely those summarized in the text above for all the 53 young butterflies tested.

Models elicited a minimum amount of attention from old males and old females, and were disregarded by all when manipulated before the roost.

VII. CONCLUSIONS CONCERNING SOCIAL BEHAVIOR

The principal conclusions to be drawn from the preceding observations and experiments on the social behavior of *H. erato hydara* are as follows:

1. Motion, odor and hue are the most important factors in courtship, and play roles both in the males and females.

2. Minor elements are size, pattern and shape.

3. Motion is the single most nearly essential element; without it neither odor nor hue can elicit courtship, and even the combination is of no value except in cases of low-threshold males mating with nearly motionless, freshly emerged females.

4. Odors function importantly as releasers in both sexes, and are apparently essential for carrying courtship to completion: no male ever tried to copulate with a model and the hindwing-flutter-elevated-abdomen response of females to models was always of short duration. Part of this, however, may have been due to the fact that the motions of the models were necessarily only rough approximations of the flutterings of live butterflies. On the other hand, motion and odor without color badges practically never elicit courtship in the male and odor alone never does. Females, however, quite readily accept courting males lacking in or different in color, providing the other elements in the pattern are represented and the female threshold is very low. Odor is certainly the primary stimulus in roosting, as it is in the non-social activity of oviposition.

5. Color badges act rather as a directive stimulus, or as a preliminary releaser at most; however in this role they are important to both sexes. Although under low threshold conditions either sex will respond with the first stage of courtship to models or individuals marked with practically any color, the most successful are those most nearly approaching the natural black marked with orange-red. The striking exception is the high sucess of all-red models, which, combined with the unimportance of pattern, indicates that the hue "red" itself is a decided releaser. (cf. the discovery of Tinbergen *et al.* (1941) concerning the supernormal black model in the grayling butterfly). The least successful of both models and painted individuals are those marked or solidly colored with hues reflecting mostly in the short-wave end of the spectrum, or colored very dark or black. Negatively ultraviolet white is rather unpredictable in eliciting responses. As might be expected, the toleration for unnaturally painted but living butterflies is wider than for odorless, clumsily moved models.

The conditions of the experimental work show that this preference for orange-red and near-by similar colors is distinctly innate, and that it is not a question of mere visibility: *H. erato* will come to paper flowers of any color except green and probe accurately. Living blue flowers of certain species, such as vervain, are visited freely, especially in the absence of more favored species. The color preference in feeding tests is distinctly for yellow first and orange second, in contrast to the species attraction for orange-red first, then orange and red, then yellow.

There was no apparent difference in social responses of butterflies conditioned to red by the sight of flowers, other individuals, or simply to their own wing colors, and those which had had no previous experience of red.

The red was of similar value in "social chasing" as in courtship, but of none in roosting.

It must be kept in mind that the "red" of *erato* is a nearly pure orange-red: its spectrum shows exceedingly low to negative reflectance in the ultraviolet, violet, blue, blue-green and green, very little in the yellow, and relatively strong in the orange and red, from 600 mμ up (Crane, 1954, p. 97, text-fig. 9a). Therefore, even if these butterflies prove to have, like bees and other insects, very weak visual sensitivity above 650 mμ, their perception of the orange region would still be adequate to make the orange components of their bands easily visible to them. The low reflectance of these bands in the yellow presumably would differentiate them adequately to the butterfly from the color appearing "orange" to human eyes; this orange, in the test material used, included moderately high reflectance in the yellow and sometimes in the yellow-green, as well as in both orange and red. It will be remembered that the color orange is not quite as attractive in *erato* courtship as a natural *erato* orange-red. However, until electroretinograms can be made of the butterflies' eyes, there seems to be no satisfactory method of determining the limits of their spectral sensitivity.

Perhaps the most interesting aspects of the results obtained are the following:

First, the selection of "red" as a releaser in courtship and social chasing indicates a secondarily evolved use of aposematic coloring. It is assumed here that aposematism in this and other red-and-black heliconiids, and their correlated development of Müllerian mimicry, occurred in evolution before the development of red as a social releaser. This is considered a likely assumption because of the widespread development of aposematism in the family. The members of the family show a variety of striking colors and patterns which very frequently do not include red, but rather browns and yellows all characterized by the inclusion of yellow and green, in addition to orange and red, in their spectral reflectances.

Second, both color pattern and secondary colors in addition to red, lack importance in social behavior, although black as a background has value. This is to be expected in a species which in other parts of its range, e.g. Surinam, is subject to conspicuous variations in pattern (Beebe, 1955).

The vitally interesting questions concerning the functions and origins of the various behavior elements, and of the relation of courtship and social behavior to phylogeny in butterflies, are left for a subsequent paper. It concerns comparative behavior in a number of species of heliconiids and is now in preparation.

VIII. SUMMARY

1. Methods of rearing and maintaining broods of the butterfly, *Heliconius erato hydara,* are described which yield healthy adults suitable for observation and experiment. The caterpillars are reared singly and fed on *Passiflora tuberosa.* The adults are maintained in large, open-air insectaries.

2. It was established by behavior responses to filtered light that *H. erato* and a number of other butterfly genera are visually sensitive to light from at least 366 mμ to at least 600 mμ.

3. Experiments involving the use of colored paper flowers of known spectral reflectances among a full series of gray models established the existence of color discrimination in *Heliconius erato.* Models representing all spectral regions as well as negatively ultraviolet white (zinc oxide) were distinguished from all grays. Yellow is the preferred color in feeding responses, and the preference appears to be innate.

4. The general habits of flight, feeding and roosting of the butterfly are described. Daily activity is governed by temperature in the early morning and by the reduction of daylight in the afternoon. As usual in butterflies, the highest activity occurs on sunny days. Feeding is most prevalent during the morning, courting in the late morning and after 2:30 P.M. Egg-laying usually occurs around noon. These *Heliconius* are entirely flower-feeders, preferring yellow and negatively ultraviolet white blossoms; a few blues are visited; reds very rarely.

5. Aposematism and defense through unpleasant odor and taste are briefly discussed.

6. Social behavior is of three types—courting, social chasing and roosting.

a. Courting depends in both sexes on both visual and scent cues. The most important visual stimuli are motion and color. Motion releasers include, in the female, air currents made by the fanning wings of the male. Color approaching in hue the orange-red of the butterfly's forewing band is an important releaser in both sexes. Minor visual releasers are form, size and pattern. At least several odors are involved, emanating at least from a special yellow gland in the tip of the female abdomen and from scent scales on the anterior margins of the male hind wings. A more general body odor is also important. Although all the releasers are mutually dependent components of the courtship pattern, motion is the one most nearly indispensable. Visual cues are more important in the early stages, odor in the later ones. Courtship cannot be initiated by odor stimuli alone.

b. Experiments with painted living butterflies and with artificial models all underline the fact that the purer orange-reds are important releasers in both sexes. A solid-color orange-red model of normal size acts as a supernormal stimulus. The farther a color lies from this region in the spectrum, the less strong is usually the response. Greens, however, are even less popular than blues. This responsiveness to orange-reds is unquestionably innate.

c. Ultraviolet appears to be of no importance in the life of this butterfly, except to the extent that its absence (e.g. in negatively ultraviolet white) affects the perception of a color for the butterfly.

d. Social chasing is common, especially among aged individuals of both sexes. Color preferences are equivalent to those characteristic of courting. No evidence of intermale threat display or of territoriality was found. Territoriality may, however, prove to occur in wild populations.

e. Odor is of great importance, color apparently of none, in roosting behavior.

f. Evidence of displacement behavior is found in atypical courting, where the proboscis is extruded.

g. It is also suggested that *H. erato,* in which the apparently aposematic scent of females develops only after mating, is evidence that the protective function of this odor developed out of a sexual function. The role of red as a sexual releaser, however, is held to be a secondary development from its original role in warning coloration.

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EXPLANATION OF THE PLATES

(Photographs by Rosemary Kenedy)

PLATE I

Courtship of *Heliconius erato hydara*: Sequence of Stages (Photographed at 1/2000 sec.)

FIG. 1. Stage I. Male approaches resting female from rear.

FIG. 2. Stage I (cont.). By rapid fluttering of wings, male sends current of air against female.

FIG. 3. Stage I (cont.). Male backs off for another forward dart. Female shows beginning of response by starting to flatten hindwings. Meanwhile her abdomen is erected, the scent gland extruded from the penultimate segment and the forewings held apposed (see Plate II, Fig. 10). Male's partly uncoiled proboscis is unusual in normal courtship (cf. Plate II, Figs. 13, 14).

FIG. 4. Stage I (cont.). Male again flutters wings against female; sometimes, as in this picture, actually touching her wings with his own.

FIG. 5. Stage II. Male moves above and toward front of female; now the scent scales on the usually overlapping margins of his fore- and hindwings are uncovered.

FIG. 6. Stage II (cont.). Note outward expansion of female hindwings, and her partly depressed antennae.

FIG. 7. Stage III. Male prepares to alight beside female. Note elevated female abdomen with extruded scent organ visible as pale spot at tip.

FIG. 8. Stage III (cont.). This is followed by copulation (see Plate III, Fig. 16).

PLATE II

Heliconius erato hydara, courtship: Details, and atypical courtship behavior.

FIG. 9. Female (right) giving partial response to courting male, Stage I: Her abdomen is elevated, the scent gland extruded and hindwings lowered and vibrated; the forewings however, are not apposed (cf. Fig. 10) (1/2000 sec.).

FIG. 10. Female giving practically full response: Characteristics of Fig. 9, plus apposition of forewings (1/2000 sec.).

FIG. 11. Male (upper) entering Stage II, showing exposed end of silver friction surfaces, bearing invisible scent scales on anterior margin of upper hindwings. Female is at left, back to camera, abdomen slightly elevated (1/2000 sec.).

FIG. 12. Courtship, Stage II, photographed by slow flash (1/200 sec.), indicating speed of male motion. Note that speed almost stops fluttering of female hindwings.

FIG. 13. Atypical courtship behavior: Male in final stages of courtship, never completed, palpates female head, thorax and forewings with his forelegs and uncoiled proboscis (1/2000 sec.).

FIG. 14. Atypical courtship behavior: Male alights in front of female, facing her, palpating her at intervals as above. Female is making partial courting responses, the scent gland partially extruded, hindwings slightly opened, forewings not apposed (1/2000 sec.).

PLATE III

FIG. 15. Setup for painting wings of living butterfly: Left, carbon dioxide cylinder with glass-topped box for anaesthetizing insect. Center, spreading board with butterfly held in place by strips of paper. Background and to right, fast-drying lacquers, solvent, and brushes for painting; ether is used for partially removing oily coating of scales before painting.

FIG. 16. A male butterfly with forewing band painted blue above, black below, copulating with normally colored female.

FIG. 17. All-red felt model butterfly being attached by insect pin to magnet on end of split bamboo wand.

FIG. 18. Black felt model with scarlet paper spots fastened to wand, being fluttered behind female, to simulate Stage I of normal male courtship (1/2000 sec.).

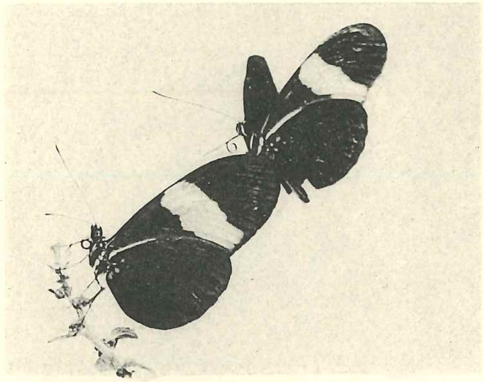
FIG. 1

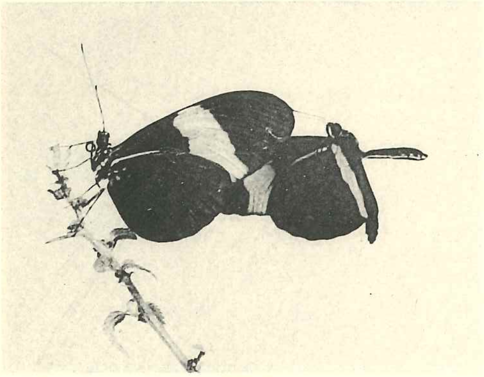
FIG. 2

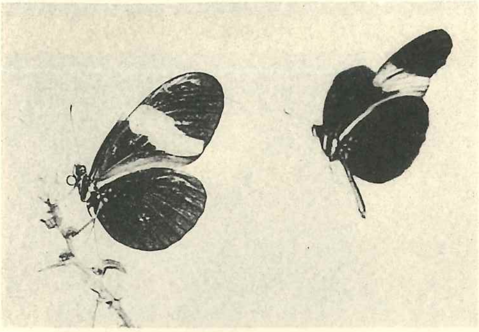
FIG. 3

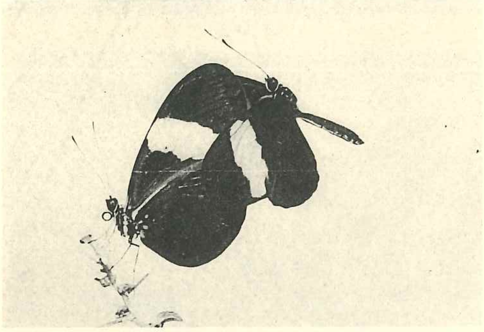
FIG. 4

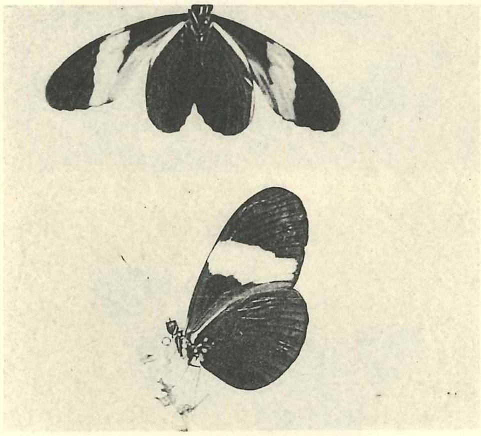
FIG. 5

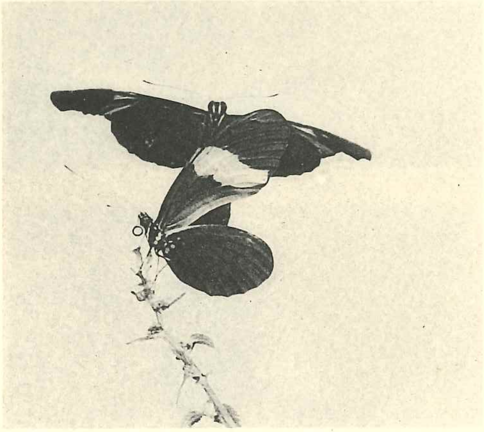
FIG. 6

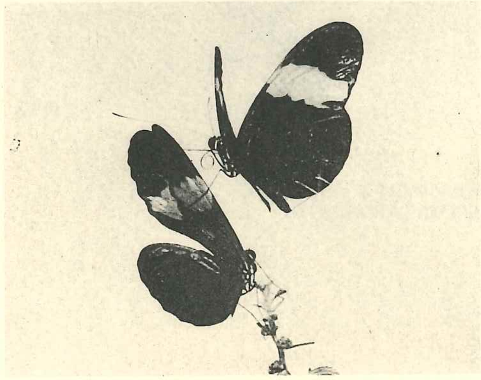
FIG. 7

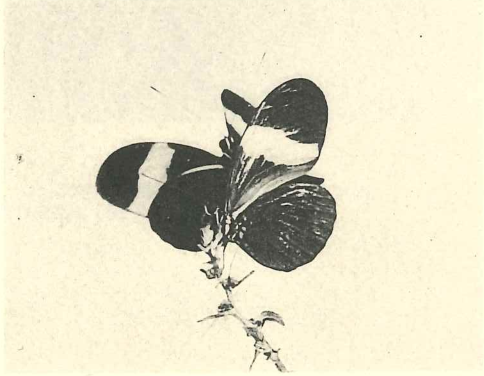
FIG. 8

IMAGINAL BEHAVIOR OF A TRINIDAD BUTTERFLY, HELICONIUS ERATO HYDARA HEWITSON, WITH SPECIAL REFERENCE TO THE SOCIAL USE OF COLOR

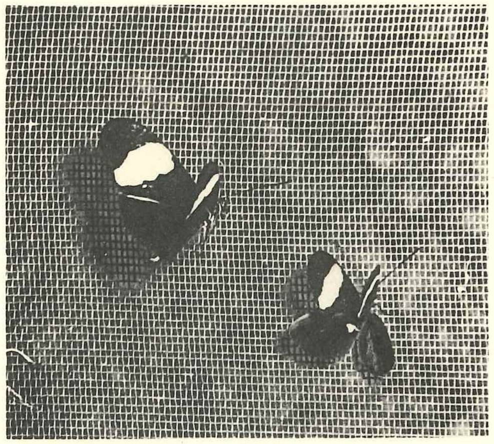

FIG. 9

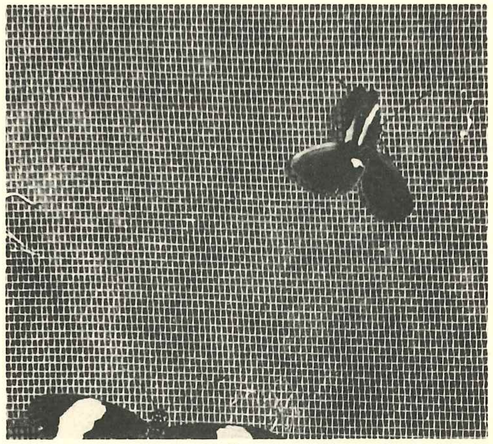

FIG. 10

FIG. 11

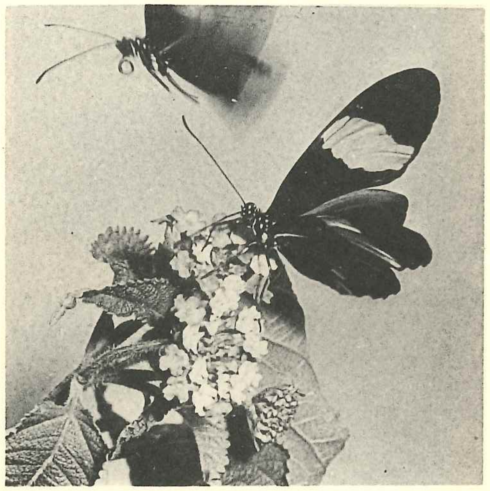

FIG. 12

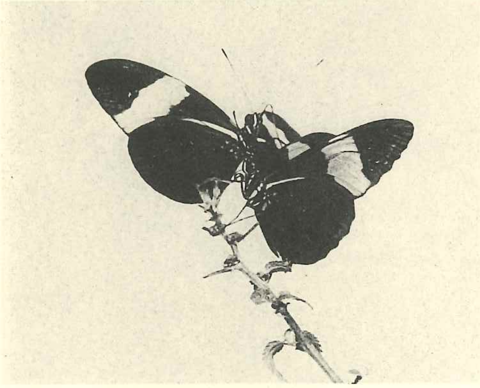

FIG. 13

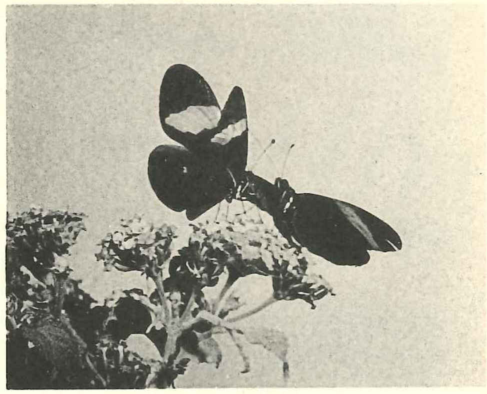

FIG. 14

IMAGINAL BEHAVIOR OF A TRINIDAD BUTTERFLY, HELICONIUS ERATO HYDARA HEWITSON,
WITH SPECIAL REFERENCE TO THE SOCIAL USE OF COLOR

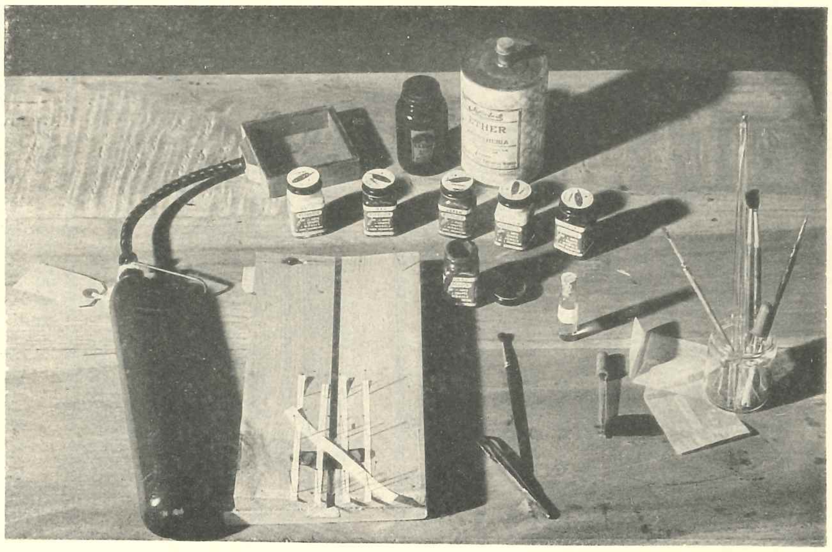

FIG. 15

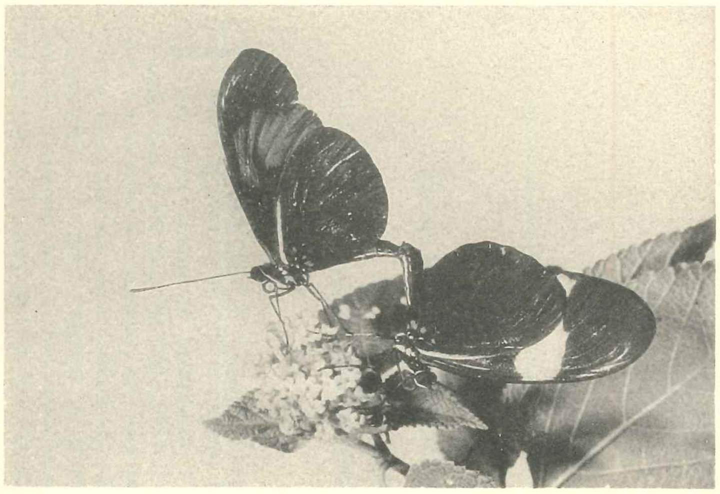

FIG. 16

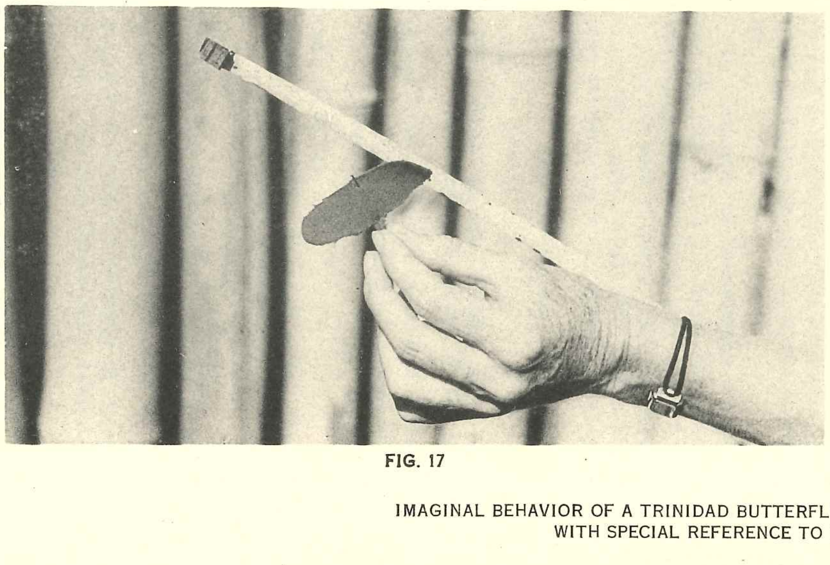

FIG. 17

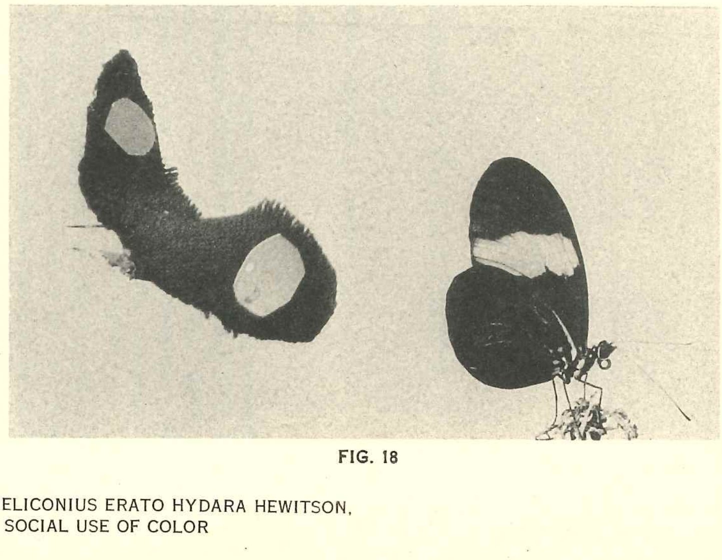

FIG. 18

IMAGINAL BEHAVIOR OF A TRINIDAD BUTTERFLY, HELICONIUS ERATO HYDARA HEWITSON,
WITH SPECIAL REFERENCE TO THE SOCIAL USE OF COLOR