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Imaginal Behavior in Butterflies of the Family Heliconiidae:
Changing Social Patterns and Irrelevant Actions¹

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(Plate I)

[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. The 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.)]

characteristic of one pattern by actions from another behavioral field.

The observations presented arose as unexpected incidental results of a comparative ethological study of six species common on the island of Trinidad, British West Indies. The publication of these data appears to be a prerequisite to the adequate exposition of comparative specific characteristics and to an illumination of the group's phylogeny. A first paper in the series, on *Heliconius erato hydra* Hewitson, has been published in which the effect of age on behavior and the occurrence of displacement behavior were mentioned (Crane, 1955). Five additional species, along with *H. erato*, are considered below. These consist of *Dryas julia julia* (Fabricius), *Heliconius melpomene euryades* Riffarth, *H. sara rhea* Cramer, *H. ricini insulana* Stichel and *H. isabella isabella* Cramer. Details of their behavior patterns, accounts of releasing mechanisms and discussion of phylogenetic aspects are being reserved for more appropriate inclusion in forthcoming contributions.

The risks of inaccuracy and incompleteness in the description of butterfly behavior became apparent very early in the work, particularly in the study of courtships. The patterns seemed at once surprisingly variable within a species, unexpectedly similar among species and altogether too unpredictable to be characteristic of arthropods, with their high degree of dependence on stereotypic forms of behavior.

Since the butterflies were being studied principally in outdoor insectaries, it was thought at first that the discrepancies might be the result of unnatural conditions—although even if that were so the interest of the variability of the behavior would scarcely have been lessened.

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I. INTRODUCTION

THIS contribution is one of a series on the biology and ecology of butterflies of the neotropical family Heliconiidae. It concerns post-imaginal changes in social behavior patterns, and various kinds of irrelevant behavior, including the displacement of actions

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Enough corroborative observations have now been made in the field, however, to show that the apparent eccentricities are equally characteristic of free-flying butterflies. Further corroboration of the natural prevalence of the types of behavior under consideration comes from the fact that, now that the causes are better understood, the patterns shown in the insectaries are highly predictable.

Some of the behavioral discrepancies have proved to be due simply to age differences in the individuals observed. The full courtship pattern characteristic of the species, for example, is elicited only in and by individuals between certain ages, although successful reproduction can take place throughout a much longer portion of imaginal life.

Other irregularities appear when, as Tinbergen (1952, p. 26) defines the conditions for displacement activities, "a strongly activated drive is denied discharge through its own consummatory act(s)." However, in the present paper the term "irrelevant behavior" (suggested by Rand, 1943) will be employed as a more general term than "displacement behavior." The latter, it seems, may be usefully restricted to the definition given by Bastock, Morris & Moynihan (1953, p. 25): "A displacement activity is an activity belonging to the executive motor pattern of an instinct other than the instincts activated."

This distinction between terms seems desirable since some of the butterfly actions under consideration do not at all appear to belong to the motor pattern of another instinct, and hence will be simply referred to as "irrelevant actions." Others, which fulfil the conditions of the more restricted definition of displacement activities, will be so designated here and treated as a subdivision of irrelevant actions.

My thanks go to the National Geographic Society for a grant-in-aid, to Dr. William Beebe, Mr. Henry Fleming and Dr. D. W. Snow for helpful suggestions, and to Miss Barbara P. Young for rearing numerous larvae.

II. HISTORICAL REVIEW

The special aspects of social behavior under consideration are little-known fields in the study of invertebrates.

The gradual development of behavior patterns in physiologically adult vertebrates has been extensively studied, and it is well known that changes occur in response to physiological alterations due both to increasing age and to seasonal causes.

Corresponding information has been gathered on few invertebrates, although the Hymenoptera include outstanding exceptions. The

sequence of changes in colony functions have been studied in worker honeybees (Rösch, 1925), *Polistes* (Steiner, 1932) and in various ants (e.g. Buckingham, 1910). Verlaine (1932) reported differences between young and old mason wasps in nest-repairing and provision behavior, that of old bees late in the season being incomplete; this observation invalidated a conclusion drawn by Fabre (1879; ed. 1920) from experiments which he performed, using aged individuals. Pardi (1947) found that age was one of the factors determining the status of individual *Polistes* females in a dominance hierarchy. Nielsen & Nielsen (1952) reported that the migratory period of a pierid butterfly (*Astia*) was confined to a single day of the five-day life-span. As an example of intrageneric variation, the parasitic wasp genus (*Opius*) may be cited: males of certain species cannot mate for five days or more after emergence, although in other species they do so early in the imaginal period (Hagen, 1953). Finally, entomologists would probably agree that female insects that have recently molted into the final instar are in general more attractive to males than are older individuals. It will be noted, however, that use of the inexact term "recently" is necessary.

Rockstein (1956) discussed the unreality of a sharp boundary between the pupal and imaginal stages in insects, citing recent research on biochemical changes occurring after emergence in the worker honeybee, house fly, *Drosophila*, moths and the Japanese beetle. In *Drosophila* there are concomitant increases in glycogen content and wing-beat frequency during the first week of imaginal life. Although this frequency change is not directly related to social behavior, the phenomenon illustrates the kind of correlation which may be brought to light in investigations linking invertebrate physiology and behavior.

Studies of irrelevant actions, including displacement behavior, in vertebrates are increasing in number, following the pioneer work of Lorenz, Tinbergen, Makkink, Koorlandt and Armstrong. General accounts and references are given by Armstrong (1950), Lorenz (1950), Tinbergen (1951, 1952), and Bastock, Morris & Moynihan (1953). Recent studies on particular species of birds and fish include those of Hinde (1953), van Iersel (1953), Moynihan (1953) and Morris (1954).

The probable occurrence of equivalent behavior in invertebrates has apparently not been suggested until recently. Armstrong (1950, pp. 379 ff.) summarized the situation as it appeared at the time of his writing as follows: "Probably displacement activities are commoner in some other groups besides birds than is at present

known, but they have reached their highest development in birds . . . So far as is at present known they have a comparatively insignificant role among insects. A thwarted solitary wasp, *Bembex rostrata*, when forced to remove pebbles repeatedly from the mouth of its burrow merely buzzed loudly and ran around in a wide arc (Nielsen, 1945). When experimenting with butterflies attracted to pieces of coloured paper Dr. D. Ilse noticed movements which might have been displacement activities (personal communication). Possibly one of the factors responsible for the apparently slower speciation of insects than birds (Mayr, 1942) is the greater displacement-proneness of the latter."

A few recent observations and comments, however, suggest that displacement activities may prove, after all, to be widespread among higher arthropods. References to date appear to be confined to the following: salticid spiders (Crane, 1949), mantids (*idem*, 1952), the butterfly *Heliconius erato* (*idem*, 1955), *Drosophila* (Bastock & Manning, 1955) and fiddler crabs, genus *Uca* (Gordon, 1955, and Crane, 1957).

III. MATERIAL AND METHODS

The studies were all conducted in out-of-door wire mesh insectaries in Trinidad (Crane & Fleming, 1953; Crane, 1955) between 1954 and 1957. During the past two seasons a new insectary, designed as were the earlier ones by Henry Fleming, has been in operation. Constructed entirely of aluminum, it measures 24 × 36 feet, the dimensions of the larger of the two earlier structures, but it is higher than its predecessor, measuring 12 feet at the ridgepole. It also has two doors with a small vestibule between, forming a baffle which has proved very useful in preventing the escape of butterflies. A small pond and bog have been added near one end; they form an efficient aid in maintaining the necessary high humidity.

The aluminum netting reflects far more heat than does bronze mesh; it also diffuses the light better, making it excellent for photography. Finally, species suitable for keeping in a cage of this size tend to bat against the netting less, even when they have just been released into it, than they did against the bronze netting of the previous insectary.

For this reason, as well as because of the insectary's relative coolness, heavy vines giving large areas of dense shade have been found to be not only unnecessary but undesirable. Instead, the planting is kept to several well-separated major groups of shrubs, saplings and wild bananas of varying degrees of height, density and leaf size. The rest of the space is occupied

by flowering weeds and by the pond. Branches with bromeliads attached stand upright at intervals against the netting, as a further aid in maintaining humidity and natural conditions. The wild banana group (*Heliconia*) beside the bog forms the coolest, most shady corner of the cage. *H. erato*, *melpomene* and other shade-lovers invariably seek it out during the heat of the day. In contrast, other species, such as *H. isabella*, which is most active around noon, frequent the open center of the cage around a group of *Lantana*, *Bidens* and *Asclepias*. In this cage all of the latter, favorite food blossoms of the heliconiids, thrive and are allowed to grow freely over most of the cage. This scattering of a natural food supply encourages a normal amount of flight by the butterflies.

The success of the new design is attested by the fact that all of the six species (p. 135) of heliconiids discussed in the present paper feed, court, mate and lay eggs. Many individuals remain alive, barring accidents, for one to three and one-half months, although differences in viability are shown. *H. isabella* is the most difficult to maintain, and observations on this species are still somewhat deficient. Two locally rare heliconiids, *Philaetrea dido* (Linnaeus) and *Heliconius wallacei* Reakirt, have not been successfully maintained. They live a few days and feed, but do not "settle in" and spend most of their active periods batting against the roof. Presumably a higher cage is needed.

Broods from all the species of heliconiids included in this study were raised in the laboratory. The young imagoes were kept in small cages out-of-doors until needed for observation or testing in the large insectary. General methods are given in an earlier paper (Crane, 1955).

Table 1 gives an idea of the number of healthy imagoes that were used in the preparation of this study. Substandard specimens, as well as those observed in the early seasons before techniques were perfected and the present problems formulated, are not included.

IV. SURVEY OF SOCIAL BEHAVIOR IN SIX SPECIES OF TRINIDAD HELICONIIDAE

The social behavior of all six of the Trinidad species discussed below consists of three general types—courtship, "social chasing" and roosting. These have already been described in some detail for *H. erato* (Crane, 1955). Except for minor differences they are characteristics of the other five species as well. Although these slight specific differences are of great potential interest from a phylogenetic point of view, their detailed discussion belongs in subsequent papers on the ethology of the genus.

TABLE I. NUMBERS OF INDIVIDUALS UPON WHICH PRESENT DATA ARE BASED (From broods reared during the seasons of 1954-1957, incl.).

Species	Males	Females
<i>Dryas julia</i>	49	46
<i>Heliconius melpomene</i>	27	28
<i>Heliconius erato</i>	71	62
<i>Heliconius ricini</i>	38	27
<i>Heliconius isabella</i>	21	22
<i>Heliconius sara</i> (1957 only)	16	19

A. COURTSHIP. Since the similarities of the behavior within the genus are far greater than the differences, a comparative chart (Table 2) of the patterns of fully developed courtship will indicate the trends to the extent needed for present purposes.

It will be seen from the table that courtship usually begins and always ends similarly in all species, while differentiation is shown principally in the first and second stages of the second, sedentary phase.

In brief summary, the sequence in its most complete form is as follows:

1. Aerial Phase.

Stage I. Nudging. A flying male approaches a resting female from the rear. She then takes wing, usually without his actually touching her in any way.

Stage II. Flight. The male chases and overtakes the female, rises above and in front of her and fans her with the rapid vibration of his wings, so spreading the products of his scent scales. She then descends or is forced down to a perch. Chases sometimes include mutual circling and spiralling in all the species. At these times the circling by the female is apparently always merely the result of her temporarily successful effort to duck out from under and behind the flying male and rise above and in front of him; he in turn repeats the manoeuvre and the resulting vertical circling may continue for several minutes. Horizontal spiralling is less frequent but seems to have a similar basis. In the previously published account of *erato* (Crane, 1955) this flight stage, which is little developed in that species and often omitted, was not separated from Stage I of the Sedentary Phase below.

2. Sedentary Phase.

Stage I. Primary Fanning. The male fans the alighted female from the front or rear, de-

pending on the species, facing in the same direction as the female. The latter, meanwhile, flutters her wings, also characteristically, elevates the abdomen and, in this stage or the next, extrudes the subterminal scent glands.

Stage II. Secondary Fanning. The male fans the female from a different position from that in Stage I, but still facing in the same direction as she. The female meanwhile extrudes the subterminal scent glands if she has not already done so.

Stage III. Alighting and Engaging. The male alights beside the female, either just in front of or just behind her, moves back or forward appropriately and, as she closes her wings, curves his abdomen up between her posterior wings, engages her genitalia with his harpes, and swings around so that the two insects now face in opposite directions.

B. SOCIAL CHASING. Discussed first in 1955, by Crane, in *erato*, "social chasing" was the term given to social flights that are not apparently directly of a sexual nature. It was found to take similar form in the other five species. In all, it consists of the pursuit of males and old females by males of any age, and of either sex by old females. It will be discussed on pp. 141 and 142.

C. ROOSTING. Four of the six species roost gregariously, namely *H. erato*, *melpomene*, *ricini* and *sara*. All return to the same bush or vine, and often to the same twigs or tendrils, night after night. Usually the perch selected is dry. Although the four species tend to maintain separate roosts, *erato*, *melpomene* and *ricini* often roost together, as do *ricini* and *sara*.

A trace of gregariousness is found in *Dryas*, which sometimes hangs up for the night near one or two others of its kind. *H. isabella*, however, always roosts alone. The two latter species always hang from beneath green leaves. Roosting will be further considered on p. 139.

V. CHANGES IN SOCIAL PATTERNS WITH AGE

None of the social behavior patterns summarized in the foregoing section is fully expressed when the insect emerges from the chrysalid, and it now appears that the maturation time for the various responses is similar in all six species. Table 3 shows these periods. "Age" indicates time after emergence from chrysalid.

It will be seen from the table that the full pattern of courtship—including Stage II of the Aerial Phase and the specifically characteristic wing flutters of the Sedentary Phase—is evinced by females only on their second and third days, that is, between 24 and about 56 hours after

where is table 2?

TABLE III. APPROXIMATE AGES AFTER EMERGENCE AT WHICH VARIOUS TYPES OF ACTIVITY OCCUR IN SIX SPECIES OF HELICONIIDS

Activity	Age
Flutters to ground when disturbed	1 hr.
First flight when undisturbed	2 hrs.
First feeding, rarely	6 hrs.
First feeding, usually	2nd day
Earliest copulation, female	10-30 minutes
Earliest copulation, male	3rd day
Complete courtship pattern elicited, female	2nd & 3rd days
Complete courtship pattern elicited, male	3rd day— 2¾ months
Latest copulation, unmated females	6th-8th day
Latest copulation, males (2 species)	2¾ months
First eggs laid	4th-12th day
Maximum ages reached, males and females (2 species)	3½ months

emergence. In *isabella*, it is not even possible to see all the specific characteristics at one time. During the female's first day, the wing flutters of the sedentary phase are very similar to those of *erato* and the aerial phase is, as usual, normally non-existent; yet by the second day the specialized flutter is already disintegrating into the more generalized *Dryas*-type flutter (see Table 2). In all the species after their third day the wing-flutterings of the females are diminished progressively in intensity and characteristic form.

In males, copulation does not occur until the third day (48 hours after emergence) and may not take place until the fourth or fifth; these later dates are apparently always characteristic of *H. sara*. No social activity by the males whatever is shown until the second day, 24 hours after emergence, when males sometimes nudge young females from the rear. After noon of the second day slight chasing may occur, but this behavior does not usually take place until the third day.

Unlike females, males court and can mate practically throughout life. In older males, although complete and successful courtship is swiftly elicited by second-day females, relatively little attention is paid to older unmated or egg-laying individuals.

Males chase each other freely throughout life, especially in the absence of young females, except during their first two days.

In both sexes and all species, roosting according to the species habit begins on the second or third night. Even in the most gregarious species (*erato*, *melpomene* and *sara*), however, young females often hang up for the night alone, unless courting or mating has proceeded during the late afternoon. At such times the female, too, often roosts with the group.

VI. IRRELEVANT ACTIONS

A. Males. Under certain conditions the courtship pattern characteristic of the various species of heliconiids becomes atypical. Instead of courtship proceeding in the usual fashion to copulation or, alternatively, to the point where one partner stops responding and both go their separate ways, the male continues special behavior that never ends in copulation. On the very rare occasions when mating soon ensues between the same partners following the first stages of this irregular behavior, the male has returned to an early stage of courtship, and then followed the typical sequence.

Irrelevant actions never begin before the male has reached Stage II of the Sedentary Phase. In other words, he is in the final phase of fanning above, in front of, or behind the alighted female, his position depending on the pattern characteristic of his species (Table 2). Sometimes the male has reached Stage III, having alighted beside the female and tried unsuccessfully to attach his harpes.

One of two major types of irrelevant behavior follows, depending on whether the female flies away and evades the male or whether she stays in place.

In the first type, having lost track of the female, the male flies about at unusual speed for up to five minutes at a time, without pausing, feeding or making any apparent "searching" motions (as he may do, on other occasions, among the vegetation). This type of behavior has been artificially induced by the observer's simply picking up the female and keeping her temporarily out of sight.

The second type of irrelevant behavior follows when the female stays alighted and often appears to the observer to be making full courting responses. The first manifestation is always poor orientation in the fanning (Pl. I, Figs. 7-8). Normally in all the species the male faces in exactly the same direction as the female, although the longitudinal axes of the two insects are usually more or less oblique to each other since the male fans characteristically from down-in-front to up-in-back. In disoriented fanning the male may face in any direction, even backward

with respect to the female, and frequently changes the direction without any regular sequence.²

After disoriented fanning has continued for any period up to five minutes in length, there are a number of alternate sequels.

Most frequently the partners separate, either the male or the female flying off, and neither one thereafter evinces either excitement or special behavior.

Ocasasionally the female takes wing and eludes the male, whereupon the male flies about rapidly as described under the first type of irrelevant behavior.

²In the study of *H. erato* already published (Crane, 1955), Plate I, Figs. 5 and 6, are excellent examples of disoriented fanning. A third example from the same series is published as Plate I, Fig. 8, of the present contribution. At the time these photographs were made, the existence of this type of irrelevant behavior had not been recognized. It is now clear that the sequence of still photographs in the earlier plate could not be taken, with present-day still camera apparatus, to illustrate a complete, normal consummated courtship between the same two individuals, photographed in sequence. This is because these courtships always proceed too swiftly to permit recharging of the speedlamp between flash shots. Only during the prolonged repetitions of irrelevant behavior can still photographs be made of a single pair during a consecutive period of courting behavior. A motion picture camera, operated at high speed, is of course suitable for the work.

In a common sequel to disoriented fanning, the male settles near the female. He may be beside her, back of her or, most frequently, facing her. He then extends the proboscis, sometimes uncoiling and coiling it repeatedly and with speed and force; when uncoiled it often touches or even palpates the female's head, thorax, legs or, rarely, abdomen (Crane, 1955, Pl. III, Figs. 13-14).

Sometimes the male palpates similarly with his antennae. In these cases the proboscis is not uncoiled.

Once only a male *Dryas*, after prolonged disoriented fanning, settled obliquely to the side of the female, facing her, and alternately brushed each of his own eyes with the palp of the corresponding side. The motion was repeated several times and the performance was repeated an hour later.

Occasionally a period of proboscis extension or antennal palpation will be followed by resumed disoriented fanning, and then a second period of the more extreme form of irrelevant behavior. Sometimes the male persists in alternate disoriented fanning and its sequels until he appears altogether exhausted and remains perched motionless nearby. At these times he cannot even be urged into flight by a sudden

close wave of the observer's hand. Under ordinary conditions such a gesture sends into the air even butterflies that are fully accustomed to moving human beings and insectary conditions.

Nine situations regularly elicit irrelevant behavior in courting males. As previously stated, an advanced stage of courtship must have been reached before irrelevant behavior begins.

1. Courting of an unmated female, four to eight hours after her emergence; that is, on the afternoon of her first day.

2. Courting of a young mated female. It is now certain that second matings in females are very rare, and are practically confined to individuals that have already reached egg-laying age and are being persistently courted by young males in the absence of young unmated females.

3. Courting of a mated female about to lay eggs.

4. Courting of a male on his first or second day.

5. Courting of a very young imago of either sex, belonging to another species.

6. Loss of an unmated female, during courtship, through her flying out of sight.

7. Courting of females, unmated or mated, more than three days old by males more than about one month old.

8. Overcrowding of the insectary. This results in somewhat indiscriminate courting activity, apparently clearly attributable to the operation of the principle of heterogeneous summation and resulting in the courting of unsuitable individuals.

9. Unresponsiveness of unmated young females, or other failure in the final stages of courtship, due to unknown causes.

B. Females. Equivalent irrelevant behavior of females following broken-off courtships has not been detected. However, later in life a female's resistance to courtship appears to change in character to such an extent that it may be termed irrelevant behavior.

A recrudescence of courtship of egg-laying females is usual in all species. Very rarely these attempts end in copulation. The usual procedure is for the male to chase the female when she is beginning to hover around the foodplant, and to try to force her to alight for the Sedentary Phase in the usual fashion. At these times the female, flying with increasing strength as she is freed of the weight of eggs, usually manages to duck out from under the flying male and fly well above him. Then, instead of flying away as unresponsive younger females do, she hovers, mounting higher as he in turn tries to come on top. As

she grows older her flight above him more and more resembles the swift, vigorous flight of the fanning male, in which the fore- and hindwings are well separated (whether or not the friction surfaces in the species concerned hold the scent scales). The male usually soon gives up and flies away, without irrelevant behavior (see p. 139).

As the female grows older she chases passing butterflies with increasing frequency, regardless of their age or sex. Some chasing of other species, either related or of similar size and color, also occurs. This behavior continues even after egg-laying has ceased and, at least in *H. erato*, is strongest in those females that have completely finished egg-laying; in that species no eggs are laid after the age of about six weeks, while the female's imaginal life often extends to more than three months. Only in the last two weeks of life does this energetic chasing decrease.

The following special behavior has been observed only in females of *H. sara*. It occurs only on the two days preceding their first egg-laying or, alternatively, when another female has already laid on the only available space. (This species in Trinidad lays eggs in a cluster on the terminal leaflets of *Passiflora auriculata*). On these occasions *sara* uncoils the proboscis and with it touches either the spot on which she would normally lay, or the eggs already laid by another female. This procedure never occurs when she is actually ready to lay her own eggs, or when no other eggs are already in place.

VII. DISCUSSION

A number of points which have emerged from the observations described in the preceding pages now require comment.

It is clear that, in this group of butterflies, there can be no accurate description of courtship or other social behavior that is based on a few observations and individuals, any more than this is possible in the case of a higher vertebrate. The ages and past experience of each butterfly observed, particularly females, must be known in order properly to describe and evaluate their activities.

A. AGE. As in many birds, the patterns of reproductive behavior are not closely linked with successful reproduction. In the first place, the full specific courtship pattern is unnecessary for copulation. Before pairing with first-day females, males omit all except Stage III of the Second (Sedentary) Phase of courtship, and the youngest females gives no overt responses at all. These exceedingly simple courtships, in which practically all appetitive behavior is almost always

omitted, seem to depend predominantly on female scent, as do courtships in moths. All specific differentiation shows in courting females later in the first afternoon and, particularly, on the second or third days. Beyond that age, unmated females are receptive for at least three to six days, although their characteristic actions decline in both intensity and specialization.

Courting of very young males by other males, or of young individuals of other species, is undoubtedly due to the strong family odor of recently emerged insects. It is interesting that this odor apparently does not develop until the insect is at least ten minutes out of the chrysalid. Once a male *H. sara* actually copulated with a female *H. melpomene* when the latter, aged about one hour, was still unable to fly. Usually these two species, which are strikingly different both in color and, even to the human sense, in odor, have very little attraction for each other.

It is unlikely that females, which spend the first day practically inactive, are often found by males during these early hours. Odor alone is not an adequate releaser. A male, after losing sight of a newly alighted young female that has slipped underneath a leaf, sometimes searches around with every appearance of vagueness and inefficiency, and only rarely locates her once again.

B. SOCIAL CHASING AND RELATED TOPICS. It now seems clear that all the activities referred to in the paper on *H. erato* (Crane, 1955) as "social chasing" are appetitive fragments of the courtship pattern. They correspond to instances in numerous other animals where, as in frogs, a male in response to an incomplete stimulus situation embraces another male and, in the absence of appropriate response, releases his grip.

It is possible that in the wild some species of heliconiids maintain territories. All that can be said now is that in this family no trace of territorial behavior, or of a dominance hierarchy, has been observed either in the insectaries or during field observations. There is no patrolling of definite routes, no special display that lends itself to an interpretation of threat behavior, no overt fighting, no individual that usually is the pursuer in the frequent inter-male chases. On the other hand all of the chases of one male by another can be explained satisfactorily as merely the chasing phase of normal courtship which, because of the inadequacy of the sexual situation, breaks down. The break usually occurs after more or less mutual circling, which exactly resembles the circling resulting from the evasion attempts of unresponsive females (p. 138). When two males are courting the same female,

the latter often escapes in the general excitement and the two males continue for a short time chasing and fanning each other. Even when, through the breakdown of the releaser sequence, they "discover" the mistake there is no evidence of agonistic behavior; the two simply separate and go their ways. Rarely one or both of the males may continue rapid flight, apparently of an irrelevant character (p. 139).

It seems likely that the phylogenetic origin of gregarious roosting was the continuation of social chasing until time to hang up for the night. This could have become fixed, through the action of natural selection, into the stereotyped patterns of the species, as it came to have protective value. Presumably the strong species odors, which laboratory tests show to be unpleasant to predators, become intensified through crowding and could be a strong deterrent to nocturnal enemies that depend largely on the sense of smell. These enemies are probably chiefly reptiles and small mammals.

The increase of chasing by older females is of particular interest. This masculine type of activity would, in a vertebrate, be subject to a hormonal interpretation, in which the decline of female reproductive hormones leads to visible effects of male hormone activity. However, in insects, morphological sexual characters, at least, are not glandularly controlled; rather "... the sex of every part is controlled directly by the chromosome constitution of the cells composing it. Hence the sexual characters are unaffected by the removal of the ovary or the testes or even by their transplantation" (Ford, 1945, p. 192). Schneirla (1953, pp. 677-678), after citing references concerning mating behavior in insects that were castrated or otherwise sexually abnormal, commented, "Such results suggest that factors governing susceptibility in male and female insects are not directly dependent upon testes or ovaries, but may concern hormones already in the blood . . . the activity of some cephalic endocrine secretion, or other physiological agencies such as neural processes." The present instance, therefore, of pseudo-masculine behavior in aged female butterflies, is one more instance of the desirability of cooperative studies between physiologists and students of behavior.

C. IRRELEVANT BEHAVIOR. Irrelevant behavior proves to play a large part in the apparently normal social life of all butterflies under observation. It is not confined to species in captivity, since it has also been frequently observed in the wild. In fact, if only a few pairs of butterflies of a given species are observed in the Sedentary Phase in the field, it is far more likely that the

observer witnesses irrelevant behavior of some kind than a specifically characteristic courtship.

The various phases of irrelevant behavior and the situations which produce it have proved to be similar in all six species. In males, it is known certainly to take place only following an advanced stage of an incomplete courtship that is directed toward an unsuitable individual. It occurs in females after their most receptive period (see preceding section). Experiments to determine whether irrelevant behavior takes place in hungry individuals that are prevented from reaching visible and olfactorily detectable food have so far been inconclusive.

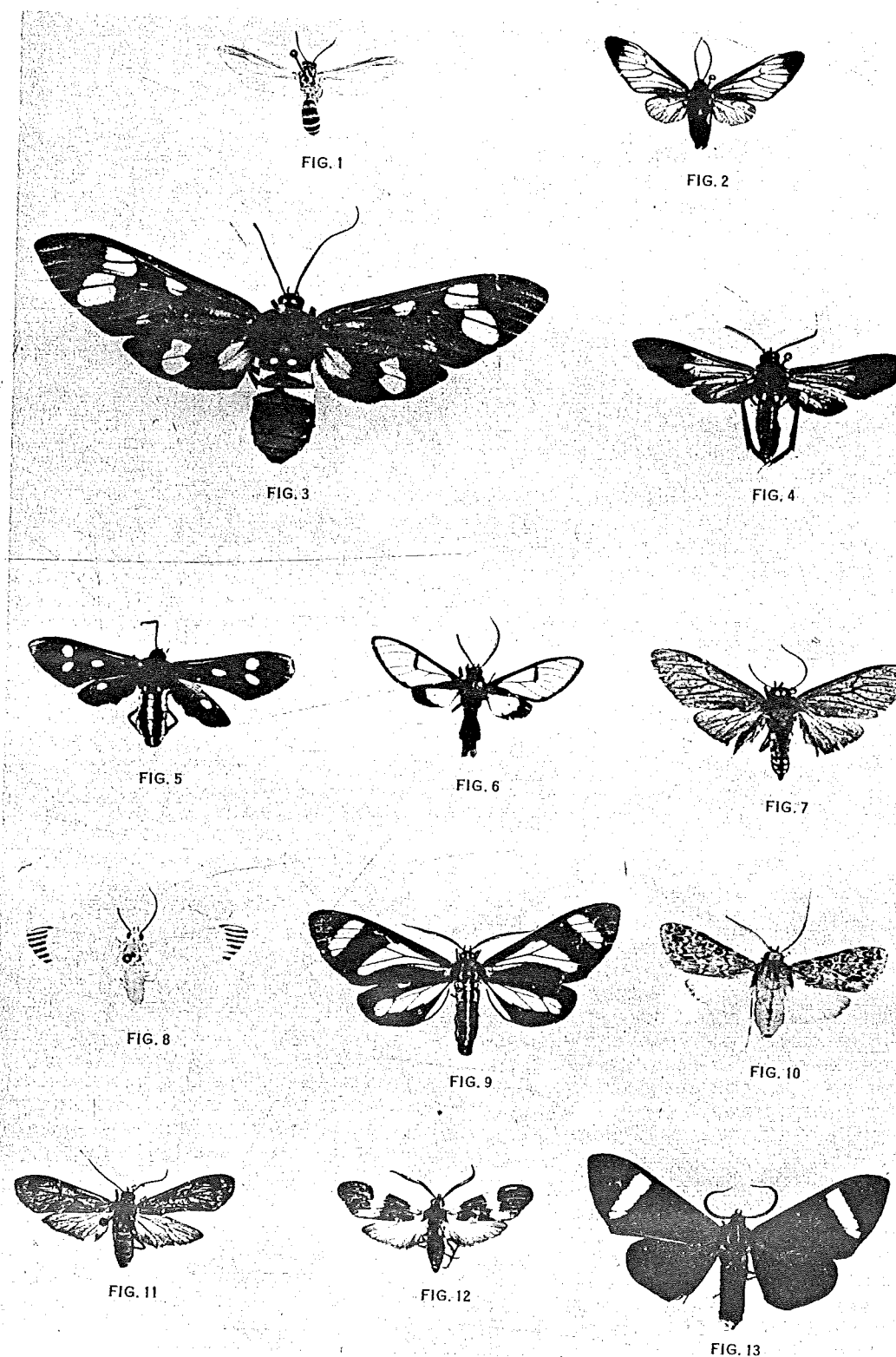
The instances of irrelevant behavior described are in completely different categories from "social chasing" since they are in no sense merely unfinished portions of the regular reproductive or roosting patterns. Like "social chasing," however, they never end in copulation.

Two of them, irrelevant proboscis-uncoiling and excessive, rapid, undirected flight, can appropriately be termed displacement activities. Occurring when the strongly activated sex drive is denied expression through its own consummatory act, the motions are clearly associated with other patterns of behavior, namely feeding and flight.

The once-observed eye-rubbing with the palps may be equivalent to the apparently displaced cleaning motions described in mantids (Crane, 1952), *Drosophila* (Bastock & Manning, 1955) and ocypodid crabs (Crane, 1957).

The two remaining types of irrelevant behavior in courting male heliconiids cannot be further classified at present. They should not, it seems, be termed displacement activities in the restricted sense (p. 136) since they do not occur in other behavior patterns found within the species. These motions are disoriented fanning and palpation of the female with the antennae. It may be, of course, that this palpation with the antennae, as well as with the proboscis, produces chemotactic sensations in a situation where the usual olfactory stimuli from the female are likely to be weak or incomplete. In the European satyrid, *Eumenis semele*, movements of the antennae form an integral part of courtship (Tinbergen *et al.*, 1943).

Disoriented fanning, in which the male may face in any direction with respect to the female, appears to be a disintegration of the normal pattern, resulting from a breakdown in the usual sequence of male-female responses. Subsequently the pattern often collapses altogether, the remaining energy being channelled into displacement-feeding or displacement-flight.



HABITS, PALATABILITY AND MIMICRY IN THIRTEEN CTENUCHID MOTH SPECIES FROM TRINIDAD, B.W.I.

In all irrelevant behavior appearing during courtship, the non-responsiveness of the female, for whatever reason, appears to be the major factor. Males that are not in a physiological condition to complete courtship simply break it off at an early stage.

As stated in earlier pages, it is now certain that females normally mate only once. Each develops a specifically characteristic odor, given off by the abdominal glands, which becomes apparent to the human observer about an hour or more after the butterflies have separated. It is the same odor given off by mated females when seized. It seems likely that it is one of the deterrents leading to irrelevant behavior when males court mated females and do not follow through to copulation even though the females are making, to the human eye, all the visible responses characteristic of the species. Another deterrent in such cases seems to be the failure of the female to fold the wings, which have been more or less flattened during the courtship fluttering, above her back when the male alights beside her in Stage III. It is impossible for him to reach her abdomen with his harpes so long as her wings are flattened.

Use of the proboscis by *H. sara*, when egg-laying is apparently thwarted, is no part of the normal egg-laying procedure of any of the members of the family that have been studied, and perhaps should be termed displacement behavior. Unlike members of some other families (Ilse, 1955 and refs.), none of the heliconiids drum the foodplant with their feet before laying.

Finally, it may be re-emphasized that almost all these types of irrelevant behavior occur in the lives of all individuals of the appropriate sexes and ages that have been studied. No reliable interspecific differences have yet been observed.

VIII. SUMMARY

Six species of heliconiid butterflies from Trinidad, B.W.I., were reared in the laboratory and their post-emergence behavior studied in insectaries. Their social behavior patterns are briefly compared.

Social responses, including courtship, vary with age. In females the full courtship pattern is elicited only on the second and third days, although they can mate successfully when both younger and older. Younger females not only give little or no overt response but draw scarcely any pre-copulatory behavior from males. Older females show progressively fewer specifically characteristic responses.

Brief chasing of males or unreceptive females by males of any age and by old females is a com-

mon form of activity. It apparently represents simply a fragment of the appetitive portion of the courtship pattern. Neither territorial defense nor inter-male threat behavior seems to be involved.

Irrelevant actions of a number of kinds are frequent. Most occur in males that are thwarted, usually by the unresponsiveness of the female, after an advanced stage of courtship has been reached. Two kinds of irrelevant actions, a disoriented type of wing-fanning and palpation with the antennae, are not known in any normal behavior pattern of the species. Other types of irrelevant behavior appear to be true displacement activities, since they occur as appropriate actions in other fields of the insects' behavior, such as in feeding and flight.

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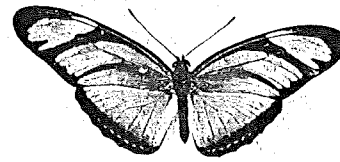
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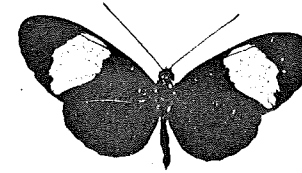
EXPLANATION OF THE PLATE

PLATE I

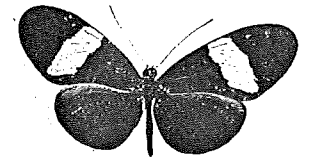
- Figs. 1-6, incl. Species and subspecies of butterflies discussed in this contribution. Photograph by Sam Dunton, New York Zoological Society.
- FIG. 1. *Dryas julia julia*. General color: Orange.
- FIG. 2. *Heliconius melpomene euryades*. General color: Black; forewing band scarlet.
- FIG. 3. *Heliconius erato hydara*. Color as in *H. melpomene*.
- FIG. 4. *Heliconius ricini insulana*. General color: Black; forewing bands pale yellow; central portion of hindwing scarlet.
- FIG. 5. *Heliconius isabella isabella*. General color: Reddish - brown to yellowish - brown; marked with black.
- FIG. 6. *Heliconius sara rhea*. General color: Black; forewing bands pale yellow; basal half of hindwing with dark blue iridescence.
- FIG. 7. Irrelevant courtship behavior in *Dryas julia*: Sedentary phase, Stage II, showing poor orientation in fanning. In normal fanning the flying male faces in exactly the same direction as the sedentary female (Table II and p. 138). Note that female has forewings almost closed as required in Stage III. However, the hindwings are still fluttering, as is characteristic of earlier courtship stages, but atypical here. Photograph by M. Woodbridge Williams, © National Geographic Society.
- FIG. 8. Irrelevant courting behavior in *Heliconius erato*, corresponding to stage shown in Fig. 7. Photograph by Rosemary Kenedy.



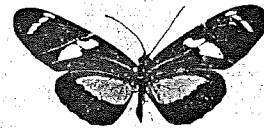
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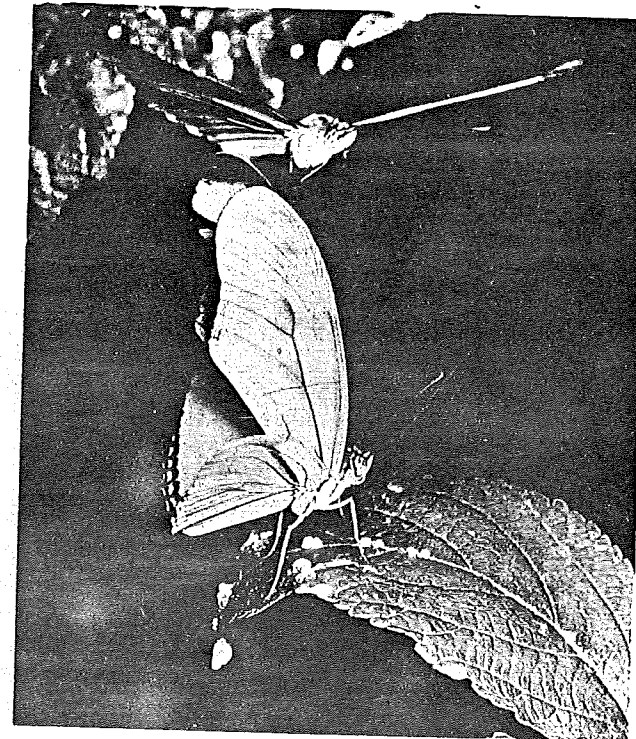


FIG. 7

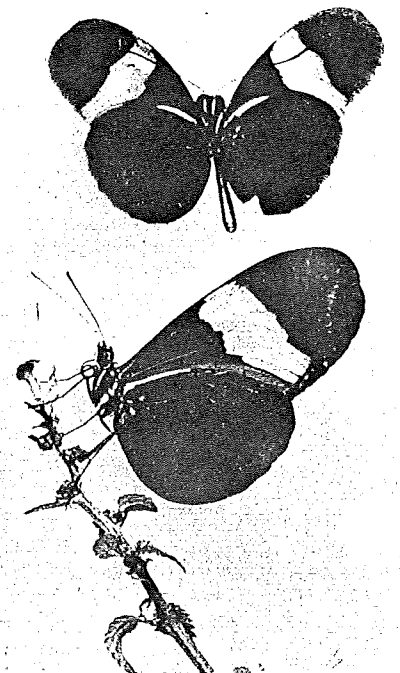


FIG. 8