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Migration of Danaidae, Ithomiidae, Acraeidae and Heliconidae (Butterflies) at Rancho Grande, North-central Venezuela.[1]

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(Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 94.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.

[For an account of Portachuelo Pass, together with a general introduction to the groups of migrating insects and migrating factors, see "Insect Migration at Rancho Grande," by William Beebe, *Zoologica*, 1949, Vol. 34, No. 12, pp. 107-110].

Migration of Danaidae.

Among the migrants through Portachuelo Pass are two members of the subfamily Danainae. The first is *Danaus plexippus megalippe*, so close to our northern monarch, *D. p. plexippus*, that it is impossible to distinguish them in flight. The second species is *Danaus eresimus eresimus*, corresponding to our northern queen, *Danaus gilippus berenice*.

The monarch is a notable migrant in the United States, but its neotropical subspecies has been considered, as in the case of many tropical birds, to be a permanent resident.

In the course of our Rancho Grande observations throughout the years 1945, 1946 and 1948 we recorded 643 *megalippe* passing southward through the Pass. A much larger number of *eresimus* was recorded, 5,254 altogether, but these were concentrated within a comparatively brief space of time, more than 5,000 on July 21.

Danaus plexippus megalippe (Hübner).

Field Name: Southern Monarch.

Species Range: North and South America and the West Indies.

Subspecies Range: Northern and western South America.

Field Characters: Unmistakable to anyone who knows the northern monarch, *D. p. plexippus*. The chief subspecific distinction is the whiteness or the tawny appearance of the forewing spots. This is impossible to detect in flying insects. In every captured migrating specimen and in those observed close at hand, at rest, the spots were *megalippe*-white. This also agrees with the geographical locale. The only possibility of confusion (and that hardly) is with the smaller and darker *Danaus e. eresimus*.

Number: Total recorded, 643. Taken, 5.

Sex: Both sexes seen and taken.

Date: April 1 to September 1.

Frequency: Mostly flying singly and fairly high, but a few closely associated groups, such as 28 on July 15, 55 with many *eresimus* on July 21, and a decided migration of 423 plus on September 1.

Condition: Most of the butterflies seemed fresh and new, a few were worn.

Non-migrant Record: Mr. Henry Fleming of the Department of Tropical Research staff reports *megalippe* as resident and breeding

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in the low Valencia plain (circa 450 meters altitude) from Limón to Maracay, and to the north of the pass at sea-level around Ocumare.

Record: 1945—July 16 (16 through pass against high wind; 12 low at km. 15). 1946—April 1 (1); May 7 (1 male alighted); September 1 (423 in fairly compact flock through pass). 1948—May 24 (5 seen); June 6 (male taken, 48737), 22 (17 seen twelve feet up), 30 (8 seen); July 5 (6 seen), 6 (15 seen), 8 (3 seen), 9 (10 very high), 10 (6 at pass; 1 taken km. 31), 15 (28 seen), 16 (12 singly), 20 (21 singly), 21 (at least 55 with large numbers of *eresimus;* 2 females taken), 26 (female taken km. 16).

Danaus eresimus eresimus (Cramer).

Field Name: Southern Queen.

Species Range: Central America to South Brazil.

Subspecies Range: Venezuela, the Guianas and northern Brazil.

Field Characters: Closely resembles *Danaus gilippus berenice,* the queen of the United States. Smaller and darker but occasionally flying with *D. plexippus megalippe.*

Number: Total recorded, 5,258. Taken, 16.

Sex: Both sexes taken.

Date: May 25 (1946); July 21 to 29 (1948).

Frequency: Only one was taken in 1946, a season of infrequent observation. In 1948 a sudden heavy migration of at least 5,000 started on July 21. Several hundred passed in early morning, increasing to several thousand from 10 A.M. on. Many seemed tired and rested on foliage and in long grass. During the succeeding eight days less numerous members of this movement were seen and taken.

Condition: Although many were weary, no worn specimens were seen.

Record: 1946—May 25 (2 taken, 46502), 28 (3 taken). 1948—June 6 (1 taken); July 21 (5,000+ seen; 9 taken), 22 (210 seen), 23 (27 in grass), 26 (1 taken), 29 (4 seen).

Migration of Lycorinae.

A single member of this second subfamily of the Danaidae used Portachuelo Pass for purposes of north to south migration.

In flight it was indistinguishable from several butterflies of other families, except on days of high winds, when flocks were forced down into the underbrush. The widely radiating scent hairs characterized it in the net or hand, rarely when resting on foliage.

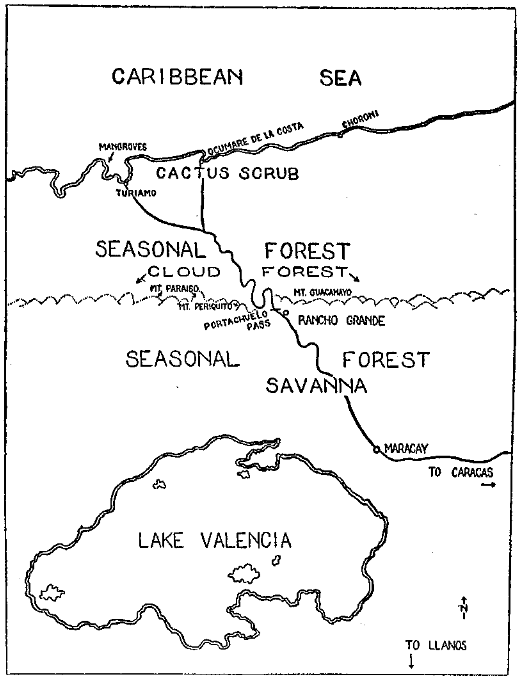
Lycorea ceres ceres (Cramer), form **atergatis** Doubleday and Hewitson.

Field Name: Tuft-scented Ithomiid-like.

Species Range: American neotropics and West Indies.

Subspecies Range: Species range, except Cuba and Haiti.

Field Characters: Considered the model for a number of mimics. Almost indistinguishable in flight from two ithomiids (*Tithorea harmonia furia* and *Melinaea illis illis*), a heliconid (*Heliconius numata*) and a nymphalid (*Protogonius hippona trinitata*).



TEXT-FIG. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

The swift, bullet-like flight of the latter removes it from too close optical confusion. Once in the hand the almost invariable protrusion of three tufts of black scent hairs identifies *Lycorea.*

Frequency: On June 6 a flurry of more than 90 large ithomiid-like butterflies drifted through the Pass, and three taken several minutes apart were all of this species. Four others showed their scent hairs while alighted on melanostomid blossoms, so it seems certain all were of the same species. Nine days later, on June 15, an identical occurrence on a smaller scale took place. A thirty-mile wind blew through the Pass and grounded a host of insects. Among these were 29 Lycoreas. On July 21 a dense flock of at least 32 passed through. Eight other flocks may well have been of this species. Eight were taken singly.

Number: Total recorded, 185. Taken, 12.

Date: April 30 to July 26.

Condition: More than half of those taken or seen showed signs of wear and tear.

Record: 1946—May 5 (1 taken at Pass). The following were taken in 1946 at or near kilometer 21: June 11 (female), 23 (female), 25 (male and female), 29 (female), 30 (female). 1948—April 30 (1 taken, 48458), 28 (1), 31 (1); June 6 (3 taken, 90 seen), 15 (2 taken, 27 seen), 26 (2); July 9 (2 taken, 10 seen), 10 (1 taken, 15 seen), 15 (1), 20 (1), 21 (1 taken, 32 in dense flock), 26 (1).

Migration of Ithomiidae.

Thirty-one species and subspecies of Ithomiidae were recorded as migrants through Portachuelo Pass.

Dr. Wm. T. Forbes lists forty-five ithomiids collected by Dr. P. J. Anduze in *"Del Norte de Venezuela."* (*Boletin de las Sociedad Venezolana de Ciencias Naturales*, VI, 1949, pp. 308-317). In the relatively minute area represented by the narrow bottle-neck of the Pass we thus took seventy per cent. of the number of ithomiids so far recorded from northern Venezuela.

In a report of the Ithomiinae of Rancho Grande by Dr. Richard M. Fox and Jean W. Fox (*Zoologica*, 32, No. 20, 1947, pp. 173-178) thirty species are listed. Of these all but three have since been recorded by us as migrants, and as these three occur within two or three kilometers of the Pass they should doubtless take their place in the migrant list. I have, however, placed them at the end of the observed migrants. In addition, four species occur as migrants which are not included in the paper by Dr. and Mrs. Fox.

From the point of view of pattern and color the thirty-one species of migrant ithomiids are much more homogeneous than the preceding family of Papilionidae or the succeeding family of Heliconidae. This makes for more difficult, or in a number of cases, impossible distinguishableness in flight.

The species fall into two general types, those typically ithomiine in yellow, black and cinnamon-rufous patterns, and those which have more or less transparent wings, with black or rufous borders. The relative proportion of species is, opaque 14 and transparent 17. This superficial division is strongly reflected and emphasized in habits. The opaque species fly in the open, at lower or higher altitudes, whereas the transparent forms are seldom found away from the shade of the jungle, usually threading their way through dense underbrush. This was especially apparent at the Pass, where a lateral shift of observation of only three or four meters, from open to heavy low growth, would mark the presence or absence of opaque-colored and of transparent patternless species.

The reality of what I have called "typically ithomiine" pattern and coloring is emphasized when we consider such migrants as the danaid *Lycorea ceres ceres*, the nymphalid *Protogonius hippona trinitata*, the heliconid *Heliconius numata numata*, the pierid *Charonias eurytale eurytale* and even the arctiid moth *Pericopis angulosa*. Again and again these unrelated forms completely fooled us in the field, we mistaking one for the other, so remarkably similar are the patterns and colors of these models and mimics.

As to relative comparison of species and individuals, of fifteen species, or about fifty per cent., one to ten individuals were recorded. One hundred to fourteen hundred specimens were observed in only five species, or twenty per cent.

Month after month there was noticed among passing migrants a large number of species comprising very few or solitary individuals. Six examples of this type of occurrence (so characteristic of many tropical organisms) are as follows, each record being made within a period of one to three hours; and all six within forty days' time.

June 17, 12	specimens	of 10	species
July 8, 12	"	" 12	"
July 15, 35	"	" 13	"
July 16, 12	"	" 10	"
July 21, 50	"	" 14	"
July 26, 22	"	" 11	"

In 1945 and 1946 Mr. Fleming was keenly interested in the composition and habits of dense flocks of ithomiids, in the vicinity of kilometers 20 and 21. The details of this interesting occurrence will soon be published. These flocks of butterflies appear earlier in the year than the first migrants and seem to be resident, but in a number of cases the comparative counts and times of occurrence link them so closely to contemporary passing migrants that I have recognized the apparent identity of origin by inclusion.

Eutresis hyperia hyperia Doubleday and Hewitson.

Field Name: Plain Hindwing.

Species Range: Central America, Colombia, Peru, Ecuador and Venezuela.

Subspecies Range: Venezuela, Colombia and northeast Peru.

Field Characters: Large semi-clear forewing, plain, pale brown hindwing. These characters sometimes apparent in flight, easily identified in resting individuals.

Number: Total recorded, 70. Taken, 24.

Sex: Both sexes taken.

Date: From April 24 to September 8.

Frequency: Recorded on 16 days, usually singly. The largest number together 28, on September 28.

Condition: Mostly fresh-appearing.

Record: 1946—April 8 (male, km. 21); July 1 (male, km. 21), 8 (male, km. 21; female, Pass); August 13 (female, km. 21); September 8 (1, 461174; 28 seen driven down to foliage by high wind). 1948—April 24 (1 taken, after being caught and dropped by blue-and-white swallow; 5 at Pass on foliage); May 1 (3), 9 (2); June 6 (5), 18 (1), 19 (1 taken, 3 seen); July 2 (1 seen), 3 (1, km. 27), 4 (1 taken, 481055; 2 seen), 10 (1 taken, 6 seen), 16 (1), 21 (1); August 2 (1).

Tithorea harmonia furia Staud.

Species Range: Trinidad, Guianas, Venezuela, Colombia, Ecuador, Bolivia and Amazons.

Subspecies Range: Venezuela and Colombia.

Field Characters: Large, typical ithomiid pattern, yellow and orange. Indistinguishable on the wing from at least three others.

Number: Total recorded, 9. Taken, 4.

Sex: Both sexes taken.

Date: From May 22 to June 16.

Frequency: A rare species. Only 9 recorded in two years.

Record: 1946—May 22 (female taken). 1948—May 24 (1 taken); June 15 (1 taken), 16 (1 caught from a group of 6, with one of which it was trying to mate. The group was all worn, alighted close together, so I am considering them of this species).

Olyris crathis crathis
Doubleday and Hewitson.

Species Range: Central America and Venezuela.

Subspecies Range: Venezuela.

Field Characters: Large, typical ithomiid pattern and color; hindwing plain red-brown with central, oblong, transparent window.

Record: Only a single specimen taken.

April 30, 1948. No. 48457. Taken on a sunny day in company of other species of ithomiids.

Melinaea lilis lilis
(Doubleday and Hewitson).

Species Range: Mexico to Colombia, Venezula and Peru.

Subspecies Range: Northern Venezuela and Colombia.

Field Characters: Large, typical ithomiid pattern and color. Except for larger size (forewing length 43 mm. as compared with 38 mm.), indistinguishable in flight from *Mechanitis doryssus veritabilis*.

Number: Total recorded, 55. Taken, 21.

Sex: Both sexes taken.

Date: April 13 to July 20.

Frequency: Seen singly or in twos, except for two groups of 16 and 18. Usually high fliers, so we doubtless missed hundreds.

Flight: Usually higher than most ithomiids.

Condition: Mostly appeared freshly emerged.

Record: 1946—April 13 (female, km. 21); June 10 (female, km. 21); July 3 (female, 46725, km. 21), 8 (2 females, km. 21). 1948—May 13 (1 taken, 48522), 15 (1), 20 (1 taken, 18 seen low and alighted), 23 (2), 26 (3); June 17 (1), 24 (1 taken with pierid and heliconid mimics); July 6 (3 taken, 16 seen close at hand in same group as those captured), 15 (1), 20 (1), 22 (1).

Xanthocleis aedesia aedesia
(Doubleday and Hewitson).

Field Name: Black Hook Ithomiid.

Species Range: Central America and northwestern South America.

Subspecies Range: Northwestern South America.

Field Characters: Large (forewing 38-40 mm.), with large black-bordered pale forewing spots, and black hook projecting downward into mid-hindwing orange. Hook easily identified in flight with naked eye or No. 7 binoculars.

Number: Total recorded, 434. Taken, 104.

Sex: Both sexes taken.

Date: April 8 to August 4.

Frequency: Decidedly gregarious, flocks recorded of 15, 19 and 41, up to 135.

Record: 1946—April 8 (male, km. 21); May 7 (male, km. 21), 21 (female), 25 (4 taken, 46502), 28 (9 taken); June 23 (3 females, km. 21); July 3 (1), 15 (3 females); August 4 (male, km. 21). 1948—April 30 (4 taken, 48455); May 4 (87 seen A.M., 48 P.M., slow, low flying), 6 (1), 9 (1), 21 (1), 23 (4), 24 (1), 29 (3); June 6 (15 taken), 7 (1), 10 (2 taken, 19 seen), 15 (2), 27 (2), 28 (6 taken, 68 seen); July 5 (1 taken, 12 seen), 6 (3 taken, 32 seen), 8 (1), 9 (41 seen high), 10 (1), 13 (1 taken, 6 seen), 15 (2 taken), 19 (2 mating), 21 (8), 23 (1), 26 (1).

Mechanitis doryssus veritabilis Butler.

Species Range: Central America and northern South America.

Subspecies Range: Venezuela and Trinidad.

Field Characters: Typical ithomiid pattern and color. Midway in size of forewing length (38 mm.) between the larger (44 mm.) *Melinaea lilis lilis*, and the smaller (28 mm.) *Hypothyris euclea fenestella*. Otherwise indistinguishable in flight.

Number: Total recorded, 133. Taken, 98.

Sex: Both sexes taken.

Date: April 29 to July 29.

Frequency: Mostly singly, otherwise in small groups of 4, 6, 7 and 18.

Condition: Very few worn specimens seen.

Record: 1946—May 28 (7 taken), 29 (5); June 23 (2 males, km. 21), 29 (male, km. 21), 30 (2 males); July 3 (1 at Pass, 46725; 3 females, km. 21), 7 (female, km. 21), 8 (female), 25 (female). 1948—April 29 (1 taken); May 6 (1, 48497), 8 (3 taken, 3 seen), 15 (1 taken, 4 seen), 23 (4), 24 (7), 26 (16), 31 (5); June 6 (6), 7 (1), 8 (1), 15 (1), 17 (2), 18 (2), 19 (1), 22 (1), 23 (1), 24 (4), 28 (4 taken from swarm of 18); July 3 (1), 4 (3), 5 (1 taken, 6 seen), 8 (1), 9 (1), 10 (1 at Pass, 1 taken, 4 seen, km. 31), 13 (1), 15 (4), 17 (1), 21 (2), 23 (1), 24 (1 at Pass, 1 at km. 15), 26 (2), 29 (1).

Hyalyris cana cana (Haensch).

Field Name: Black-bordered Clearwing.

Species Range: Venezuela and Colombia.

Subspecies Range: Eastern Colombia and northern Venezuela.

Field Characters: This rare ithomiid is very distinct and easy to distinguish both on the wing and alighted. The wide, white-dotted border surrounding all four wings, enclosing transparent central areas, is unmistakable. Indistinguishable from the congeneric *H. coeno*.

Number: Total recorded, 7. Taken, 7.

Sex: Both sexes taken.

Date: July 14 to 21.

Frequency: Very remarkably, in 1948, seven specimens were taken, one a day, July 18 being the only exception to the regular sequence, no insect being captured on this date. They were low-flying, close to the top of the low growth like the other clearwings.

In addition to the 1948 migrants at the Pass, Mr. Fleming took 4 males and a female in the dry season, at kilometer 21. These seemed to be residents, judging by the dates of capture, and were associated with a large swarm of ithomiids of other species. They were taken on February 27 and March 4.

Record: 1948—July 14 (1 taken), 15 (1, 481174), 16 (1 taken), 17 (1), 19 (1), 20 (1 taken at ginger blossoms), 21 (1).

Hypothyris euclea fenestella (Hewitson).

Field Name: Dwarf Typical Ithomiid.

Species Range: Central America, Colombia, Venezuela, Ecuador and Peru.

Subspecies Range: Venezuela and Trinidad.

Field Characters: Typical ithomiid yellow, orange and black. Differs in its small size from other similarly colored species. From the equally numerous and equally sized *Ithomia iphianassa* it differs in lacking the transparent large spots and oblong windows.

Number: Total recorded, 488. Taken, 123.

Sex: Both sexes taken.

Date: April 29 to August 2.

Frequency: One of the most abundant species and decidedly gregarious, counts of 54 to 266 being made, and of course many thousands of butterflies missed. On a number of days this was the dominant species.

Record: In 1946 Mr. Fleming collected 35 males and 56 females in the vicinity of kilometers 20 and 21. 1948—April 29 (1, 48449); May 21 (2), 23 (1), 25 (14 taken, 54 seen), 26 (2), 29 (1), 31 (1); June 6 (14 taken), 15 (1), 16 (1 taken, 12 seen), 17 (1), 21 (3), 22 (1), 24 (2), 27 (2); July 3 (2), 4 (6 taken, 28 seen), 5 (5 at Pass, 3 taken km. 21), 8 (13 taken, 266 seen), 10 (3 taken, 3 seen), 13 (1 taken, 2 seen), 14 (4), 15 (9), 16 (1), 20 (3), 21 (16), 23 (1), 26 (3), 29 (5); August 2 (2 taken).

Ithomia agnosia agnosia Hewitson.

Species Range: Venezuela, Colombia and northern Peru.

Subspecies Range: Venezuela.

Field Characters: This clearwing was quite indistinguishable from seven or eight other species.

Number: Total recorded, 23. Taken, 23.

Sex: Both sexes taken.

Date: April 30 to September 3.

Frequency: Solitary flyers and low, just clearing the undergrowth.

Record: Only 4 migrants were taken at the Pass in 1948, whereas eighteen were taken at kilometers 20 and 21 in 1946. Dates corresponding as to months, I have included the latter as probable migrants.

1946—April 30 (1); May 15 (1), 24 (1), 26 (1), 28 (1); June 4 (2), 7 (1), 14 (1), 18 (1), 23 (1), 25 (1), 26 (2); July 2 (3), 17 (1); September 3 (1). 1948—May 26 (1); July 6 (1), 26 (2 taken).

Ithomia iphianassa iphianassa Doubleday and Hewitson.

Field Name: Common Small Ithomiid.

Species Range: Venezuela.

Subspecies Range: Venezuela.

Field Characters: The small size combined with transparent patches and bright colors make this very abundant species easy to identify in flight.

Number: Total recorded, 1,403. Taken, 205. Many thousands must have passed unrecorded.

Sex: Both sexes taken.

Date: April 27 to September 8.

Frequency: This species was so abundant that on some days a continuous stream was passing. No condensed flocks but the dominant butterfly on many days. The low counts at the Pass in 1946 due to infrequent observation.

Flight: Moderately low and never very rapid.

Record: 1946—May 28 (1), 29 (1); July 3 (2), 17 (1); September 7 (4), 8 (3). In addition 109 males and 37 females were taken by Mr. Fleming at kilometer 20 and lower in 1946. 1948—Records are so numerous that I condense as follows: April 8 (1 taken, 8 seen), 28 (7 seen); May (on 17 days, 33 taken, 98 seen); June (on 30 days, 97 taken, 175 seen); July (on 28 days, 75 taken, 925 seen).

Mileria cymothoë (Hewitson).

Field Name: Small Clearwing.

Species Range: Venezuela and Colombia.

Field Characters: Small and almost completely transparent, indistinguishable in life from 5 or 6 other species.

Number: Total recorded, 12. Taken, 12.

Sex: Both sexes taken.

Date: May 5 to July 21.

Record: 1948—May 5 (1 male), 6 (1 male), 23 (1 male), 26 (5 females), 29 (1 male); June 6 (male), 28 (female); July 21 (female).

Oleria victorine graziella (Oberthür).

Species Range: Central America, Colombia, Venezuela, Ecuador, Bolivia and upper Amazons.

Subspecies Range: Venezuela and Colombia.

Field Characters: A small clearwing with strong black borders, indistinguishable in life from six other species.

Number: Total recorded, 7. Taken, 7.

Sex: Both sexes taken.

Date: April 8 to July 10.

Record: 1946—April 8 (2), 13 (1), 16 (2); July 10 (1). 1948—May 29 (1).

Oleria makrena makrena (Hewitson).

Species Range: Colombia, Venezuela and Ecuador.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: A clearwing with wings tinted with whitish. Only once could I be sure of it before capture; in the sunlight resting on a leaf.

Number: Total migrants, 7. Taken, 7.

Sex: Both sexes taken.

Date: June 6 to July 21.

Record: At lower levels in 1946 Mr. Fleming took 51 males and 21 females. These may very likely have been early migrants but we had no definite proof. 1948—June 6 (1), 15 (1), 16 (1); July 5 (1), 6 (2 seen alighted), 8 (1), 21 (1).

Oleria phemonoë phemonoë (Doubleday and Hewitson).

Species Range: Colombia, Venezuela and Brazil.

Subspecies Range: Venezuela.

Field Characters: A rare clearwing indistinguishable in life from related species.

Number: Total recorded, 11. Taken, 11.

Sex: Both sexes taken.

Date: May 29 to July 23.

Record: 1946—April 8 (2, km. 21); May 29 (2 at Pass); June 20 (female, km. 27); July 5 (male, km. 27), 28 (female, km. 27). 1948—May 27 (1 at Pass); July 8 (1), 23 (2).

Aeria eurimedia agna Godman and Salvin.

Field Name: Six-lemon-striped Ithomiid.

Species Range: Central America, Colombia, Ecuador, Venezuela, Guianas and Amazonia.

Subspecies Range: Central America, Colombia, Venezuela and Trinidad.

Field Characters: The six elongate lemon spots surrounded by spots make this small species easy to identify even in flight.

Number: Total recorded, 56. Taken, 29.

Sex: Both sexes taken.

Date: April 7 to September 7.

Record: 1946—Twenty specimens taken at or near kilometer 20, undoubtedly migrants; dates as follows: April 7, 8, 13, 30, May 28, June 10, 16, 30, July 3, 17, 25, 28, August 13, September 7. 1948—May 25 (2 taken, 16 seen), 26 (1); June 6 (2), 9 (1), 22 (1 taken, 11 seen); July 5 (1), 8 (1).

Dircenna euchychma Felder.

Species Range: Colombia and Venezuela.

Field Characters: A medium sized, translucent, dusky, red-brown species, indistinguishable in life from *Dircenna jemina.*

Number: A single specimen, 481392, taken July 26, 1948, migrating through Pass in company with ithomiids of other species.

Dircenna jemina (Geyer).

Species Range: Venezuela and Colombia.

Field Characters: A medium, smoky-brown, translucent species recognizable in life only when it has alighted close by.

Number: Total recorded, 52. Taken, 18.

Sex: Both sexes taken.

Date: March 15 to July 21.

Frequency: Taken and seen singly, except on March 15, April 27 and May 13, when 12, 16 and 6 individuals were seen resting close together just beyond reach.

Record: 1946—May 3 (1), 13 (1); June 26 (1), 29 (1), 30 (1); 1948—March 15 (1 taken, 12 seen), April 27 (2 taken, 16 seen), 29 (1); May 5 (1), 6 (1), 13 (1 taken, 6 seen); June 17 (1); July 8 (1), 13 (1), 16 (2), 21 (1).

Ceratinia tutia tutia (Hewitson).

Species Range: Central America, Colombia and Venezuela.

Subspecies Range: Venezuela and Colombia.

Field Characters: A small, smoky-brown, translucent species not distinguishable from *Hypoleria* and *Godyris.*

Number: Total recorded, 237. Taken, 19.

Sex: Both sexes taken.

Date: May 26 to August 7.

Frequency: Seen and taken singly except on August 8, 1946, when a cloud of this species came up to the Pass, after heavy rain, and alighted near by. I took 3 and counted 218.

Record: 1946—August 8 (3 taken, 218 seen), 12 (1). (Fourteen males and 2 females taken at kilometer 20 or lower, not counted as migrants). 1948—May 26 (2); June 6 (1), 7 (1), 9 (2), 12 (1), 15 (1), 16 (1), 24 (1), 28 (2); July 8 (1), 13 (1), 21 (2).

Episcada hymenaea (Prittwitz).

Field Name: Small Brown-veined Clearwing.

Species Range: Widely distributed in South America.

Field Characters: A very small, brown-veined, patternless clearwing, not distinguishable in life from *Mileria* or *Pteronymia aletta.*

Number: Total recorded, 44. Taken, 44.

Sex: Both sexes taken.

Date: May 21 to July 26.

Breeding Note: Female No. 48592, taken May 25, contained many fully formed eggs, with surface sculpture, including vertical grooves and finer markings apparent.

Record: 1946—May 28 (1); June 26 (male, km. 20), 29 (2 males, km. 20). 1948—May 21 (3), 23 (3), 24 (3), 25 (10), 26 (7), 29 (3); June 6 (4), 17 (1), 18 (1); July 10 (1), 15 (1), 21 (2), 26 (1).

Episcada sylpha Haensch.

Species Range: Venezuela.

Field Characters: Indistinguishable in life from *Episcada hymenaea,* but very rare.

Number: Two specimens only, 1946, June 29, male; and 1948, May 30, male.

Hypoleria ocalea (Doubleday and Hewitson).

Species Range: Colombia, Venezuela and Trinidad.

Field Characters: Small, half smoky, half transparent; not distinguishable in life from other similar species.

Number: Total recorded, 4. Taken, 4.

Date: May 26.

Record: 1948—May 26 (4 taken).

Pteronymia adina Hewitson.

Species Range: Venezuela.

Field Characters: A small clearwing, indistinguishable from others in life.

Number: Total recorded, 4. Taken, 4.
Sexes: Both sexes taken.
Date: May 21 to July 20.
Record: (2 males and 11 females taken in March by Mr. Fleming at kilometer 20 and lower. Owing to early date not counted as migrants). 1948—May 21 (1), 25 (1); June 6 (1); July 20 (1).

Pteronymia aletta (Hewitson).

Species Range: Venezuela.
Field Characters: A very small, pale smoky clearwing, hardly to be distinguished in life from several others.
Number: Total recorded, 7, Taken, 7.
Sex: Both sexes taken.
Date: May 24 to July 15.
Record: 1946—June 7 (1), 23 (1 taken, km. 20). 1948—May 24 (1), 25 (2), 29 (1); July 15 (1).

Pteronymia asopo (C. and R. Felder).

Species Range: Northern Colombia and Venezuela.
Field Characters: Small clearwing with large white splash. Not identifiable in life.
Number: Total recorded, 11. Taken, 11.
Sex: Both sexes taken.
Date: April 20 to July 17.
Record: 1946—April 20 (2 taken); June 29 (2 taken). 1948—June 17 (3 taken), 18 (1), 22 (1), 24 (1); July 10 (1 taken, km. 20).

Pteronymia beebei Fox and Fox.

Species Range: Northwestern Venezuela.
Field Characters: Medium clearwing. Not distinguishable in life from several other species.
Number: Total recorded, 14. Taken, 14. (All taken at Pass).
Sex: Both sexes taken.
Date: May 25 to August 5.
Record: 1946—August 5 (1 taken at Pass). Thirty-seven males and 7 females, including type of species, taken by Mr. Fleming at kilometers 18 to 21. 1948—May 25 (1), 26 (3), 29 (1); June 6 (1); July 8 (1), 15 (2), 16 (1), 21 (1), 26 (1); August 2 (1).

Pteronymia nubivaga Fox and Fox.

Species Range: Northwestern Venezuela.
Field Characters: Small clearwing, indistinguishable in life from several other species.
Number: Total recorded, 14. Taken, 14.
Sex: Males only taken.
Date: April 14 to July 8.
Record: 1946—April 14 to July 8 (12 males, taken by Mr. Fleming around km. 20). 1948—May 9 (2 taken at Pass).

Pteronymia veia (Hewitson).

Field Name: Yellow-spotted Clearwing.
Species Range: Venezuela.
Field Characters: Small clearwing with bright yellow spot.
Number: Total recorded, 44. Taken, 44.
Sex: Both sexes taken.
Date: May 6 to August 2.
Frequency: Usually single, but now and then several in association. As with all clearwings they fly low, slowly, just above or more usually threading through underbrush.
Record: 1946—May 28 (1 taken at Pass). 41 males and 11 females taken by Mr. Fleming around kilometer 20 and lower, in 1946. Not counted as migrants, in spite of circumstantial evidence. Extreme dates March 8 to July 15. 1948—May 6 (1), 9 (1), 21 (1), 24 (1), 25 (1), 26 (1), 29 (1), 31 (1); June 6 (5), 15 (1), 17 (2), 18 (1), 22 (3), 27 (2); July 5 (1), 7 (1), 8 (2), 13 (1), 14 (1), 20 (1), 21 (3), 23 (1), 26 (3), 28 (1); August 2 (1).

Godyris kedema kedema (Hewitson).

Species Range: Venezuela and Colombia.
Subspecies Range: Venezuela.
Field Characters: Medium, pale smoky, half transparent. Often flies so slowly and low that identification is possible.
Number: Total recorded, 21. Taken, 21.
Sex: Both sexes taken.
Date: May 21 to August 2.
Record: 1946—June 7 (1 taken at Pass). Seventeen males and 14 females collected by Mr. Fleming at low altitudes to the south of Pass, around kilometer 20, in 1946. Extreme dates were March 13 and August 4. 1948—May 21 (1), 25 (1), 29 (2), 31 (1); June 6 (1), 9 (1), 28 (1); July 13 (1), 15 (5), 17 (1), 21 (2), 26 (3); August 2 (1).

Pseudocada timna (Hewitson).

Species Range: Colombia and Venezuela.
Field Characters: Small clearwing, with much white on forewing. Not distinguishable in life from several others.
Number: Total recorded, 7. Taken 7.
Sex: Both sexes taken:
Date: May 6 to July 15:
Record: 1946—None taken at Pass. At kilometer 20, Mr. Fleming collected 16 males and 2 females, the extreme dates being April 8 and July 15. 1948—May 6 (1), 24 (1), 25 (2), 29 (1); June 24 (1); July 15 (1).

Hymenitis andromica andromica (Hewitson).

Species Range: From Guatemala south through Colombia, Venezuela, Ecuador, Peru and Bolivia.
Subspecies Range: Venezuela and Colombia.
Field Characters: Medium clearwing with considerable white on forewing. Indistinguishable from others.
Number: Total recorded 21. Taken 21.
Sex: Both sexes taken:
Date: May 24 to August 2.
Record: 1946—July 3 (1 taken); August 1 (1 taken at Pass from flock of 19, probably the same species). At kilometer 20 and lower, in 1946, Mr. Fleming collected 66 males and 43 females, doubtless migrants, but not counted as such. 1948—May 24 (2), 25 (4), 29 (1); June 6 (2), 9 (1), 22 (1), 28 (1); July 8 (1), 13 (1), 14 (1), 15 (1), 16 (1), 24 (1), 26 (2); August 2 (1).

Hymenitis dercetis
(Doubleday and Hewitson).

Species Range: Venezuela and Colombia.
Field Characters: Medium clearwing, bright yellow splash. Indistinguishable from several others.
Number: Total migrants reported, 31. Taken, 31.
Sex: Both sexes taken.
Date: April 30 to September 5.
Record: 1946—May 28 (1 taken at Pass), September 5 (1 taken). At kilometer 27 and lower, Mr. Fleming collected 72 males and 12 females. 1948—April 30 (1); May 1 (2), 9 (2), 24 (2), 25 (1), 26 (2), 29 (1), 31 (1); June 6 (2), 11 (1), 15 (2), 17 (1), 24 (1), 27 (1), 28 (1); July 3 (1), 10 (1 taken, many probably of this species, seen), 15 (3), 16 (1), 17 (1), 21 (1).

PROBABLE MIGRANTS BUT NOT TAKEN AT PASS.

Athesis clearista clearista
(Doubleday and Hewitson).

Field Name: Semi-transparent Clearwing.
Species Range: Colombia and Venezuela.
Subspecies Range: Venezuela.
Field Characters: A medium, orange-veined clearwing, very similar to several other species.
Record: Two male specimens only taken, and neither actually at the Pass. Two males, 46106, taken February, at Red Bridge, less than one kilometer from the Pass, but in the dry season.

Hyalyris coeno coeno
(Doubleday and Hewitson).

Species Range: Nicaragua, Colombia, Peru and Venezuela.
Subspecies Range: Venezuela.
Field Characters: Indistinguishable in life from *Hyalyris cana*.
Record: Not taken actually at Pass. In April, 1946, 3 males, 1 female, taken at kilometer 27, north of Pass, feeding on flowers.

Callithomia agrippina alpho
(C. and R. Felder).

Species Range: Panama, Colombia and Venezuela.
Subspecies Range: Eastern Colombia and Venezuela.
Field Characters: A smoky clearwing not distinguishable in life from several other species.
Record: No specimens taken at Pass and only one near by but lower. A female, at kilometer 21, June 23, 1946.

MIGRATION OF ACRAEIDAE.

The members of this small family seem always to appear at the Pass on days of intensive migration, and in life they are so similar to the smaller ithomiids, as well as to many heliconids, that they were caught and enveloped without special attention. Later, when their true nature was discovered in the laboratory, it was too late to recall flight characters or to be certain of how many others had passed unobserved.

Actinote anteas (Doubleday and Hewitson), forms **anteas** (Doubl. and Hew.) and **straminosa** Jordan.

Field Name: Striated-hindwing Ithomiid-mimic.
Species Range: Guatemala to Colombia, Venezuela, Trinidad and Tobago.
Field Characters: Inconspicuous in flight, closely resembling the smaller opaque ithomiids, and even more exactly the heliconid *Heliconius vibilia vialis*.
Number: Total recorded, 32. Taken, 32.
Sex: Both sexes taken.
Date: April 29 to July 26.
Record: 1946—July 3 (1 taken). 1948—April 29 (1 taken), 30 (2); May 4 (1), 21 (2, 48546), 23 (3); June 6 (1), 27 (1, 48966); July 3 (1, 481541), 6 (1), 13 (1), 15 (7), 16 (1), 21 (2), 26 (2).

Actinote hylonome Doubleday.

Field Name: Small White-banded Black.
Species Range: Venezuela and Colombia.
Field Characters: Small, black, with wide oblique band across each forewing. So resembles other small butterflies and even day-flying moths, that only once were individuals noticed, other than those captured.
Number: Total recorded, 20. Taken, 12.
Date: April 27 to July 16.
Record: 1948—April 27 (2, 48378, 48398; 8 others seen); May 9 (1), 23 (2, 48573), 25 (1), 26 (2); June 6 (1); July 3 (1), 8 (1), 16 (1).

MIGRATION OF HELICONIDAE.

Of all groups of butterflies the heliconids are nearly the most difficult in which to designate typical patterns or colors. In this respect the eighteen species and subspecies of heliconid migrants through Portachuelo Pass seem to have evolved in an effort to resemble species in other groups, to offer themselves as models or mimics, or at least to have developed intensely independent and individual forms.

This, combined with the habit of low flight and slow flapping with much leisurely gliding, makes sight identification in most species a very easy matter.

A key based on pattern and color was of the greatest help in day-by-day recording of numbers, and for what it may be worth to others I reproduce it here. It was of course intended only for my own use with the migrants at Rancho Grande.

Heliconia Sight Identification Pattern and Color Key.

Fritillary-like (northern genera; *Agraulis, Argynnis*, etc.)
  Silvery Fritillary—*Agraulis vanillae*
  Dark Silvery Fritillary—*Dione juno*

Large Orange Fritillary—*Dryas iulia*
Dwarf Orange Fritillary—*Heliconius aliphera*
Yellow-banded, Red-hindwing
Solid-red-hindwing—*H. procula*
H. clysonimus
Striated-red-hindwing—*H. doris* (form, *transiens*)
Yellow-banded, Blue-hindwing
Large, Blue-hindwing—*H. doris* (form, *doris*)
Small, Blue-hindwing—*H. sara*
Light-striped Black
4-white-striped Black—*H. antiochus antiochus*
4-yellow-striped Black—*H. antiochus aranea*
Zebra-striped Black—*H. charithonius*
Red-banded Black—*H. melpomene*
Acraeid-mimic—*H. vibilia vialis*
Ithomiid-mimic—*H. isabella dynastes*
H. anderida holcophorus
H. anderida semiphorus
H. eucoma metalilis
Green-spotted—*Philaethria dido*

Agraulis vanillae vanillae (Linnaeus).

Field Name: Southern Fritillary.
Species Range: New York to Chile and Argentina.
Subspecies Range: Panama, northern South America, Amazonia and Lesser Antilles.
Field Characters: The same species as our northern silver spangled fritillary, but several minor characters provide it with a subspecific name, characters impossible to tell on the wing. All specimens taken were characteristic, however. The absence of the dark hue of the underwings easily distinguishes it from *Dione juno*.
Number: Total recorded, 188. Taken, 40.
Sex: Both sexes taken.
Date: May 9 to July 29.
Frequency: Usually singly or in twos. On June 22 and 24 great numbers were observed high in air, hundreds of which must have escaped our counts.
Condition: A minority only were observed to be torn and faded.
Record: 1946—May 28 (1), 25 (1). 1948—May 9 (2 seen), 13 (2), 15 (1 taken, 4 seen), 23 (2); June 6 (13), 17 (2), 22 (many high, 19 counted), 24 (many high, 64 counted); July 2 (2), 5 (1), 6 (11 seen), 8 (2 taken, 17 seen), 10 (1), 13 (1, km. 15), 14 (1), 15 (3), 16 (4), 17 (2, km. 30; 15 seen), 19 (2), 21 (1), 29 (14 seen).

Dione juno (Cramer).

Field Name: Dark Silvery Fritillary.
Species Range: Central America to Brazil.
Field Characters: Distinguished from *Dryas iulia* above by broader, darker wings and smaller size, and from *Agraulis vanillae* below by dark setting of silver spangles.
Number: Total recorded, 194. Taken, 19.
Sex: Both sexes taken.
Date: May 25 to September 9.
Frequency: Decidedly gregarious, but in moderately sized flocks.
Condition: Many worn and tattered specimens, many perfectly fresh.
Record: 1946—September 9 (1 taken). 1948—May 25 (1 taken, 8 seen); June 17 (2 taken, 14 seen); July 1 (1 taken, 12 seen), 5 (1 taken, 10 seen), 9 (48 seen high), 10 (1 taken, 19 seen), 11 (2 seen, km. 31), 14 (1 taken, 3 seen), 15 (1, km. 15), 16 (1), 17 (8 seen), 19 (2 taken, 9 seen), 22 (1 taken, km. 35, 28 seen), 29 (21 seen).

Dryas julia (Fab.).

Field Name: Large Orange Fritillary.
Species Range: Trinidad, Guiana and Brazil. Not before recorded from Venezuela.
Field Characters: A large, narrow-winged orange fritillary, to be confused only, and that hardly, with the silver-spangled *Dione juno*.
Number: Total recorded, 969. Taken, 6.
Sex: Both sexes taken.
Date: April 15 to September 7.
Frequency: On July 18, September 1 and 7, 1946, seven-eighths of all observed specimens of this species passed through the Pass. In the following year only flocks of moderate size were seen.
Condition: In many of the flocks the fresh and the worn and faded individuals seemed about equal in number.
Record: 1946—May 28 (1); July 18 (450 + seen), September 1 (321 counted), 7 (95 + counted). 1948—April 15 (1), 30 (4 seen); May 4 (3 seen); June 28 (1 taken, 22 seen); July 3 (1 taken, 28 seen), 10 (2 seen, km. 20), 13 (1 taken, km. 15), 17 (3 seen), 21 (4 seen), 24 (2, km. 31), 26 (42 seen), 29 (16 seen).

Heliconius aliphera aliphera (Godart).

Field Name: Dwarf Orange Fritillary.
Species Range: Mexico to Paraguay.
Subspecies Range: Colombia and Peru to Trinidad and Paraguay. Not before reported from Venezuela.
Field Characters: A diminutive copy of the preceding species, *Dryas julia*.
Number: Total recorded, 2,313. Taken, 35.
Sex: Both sexes taken.
Date: May 28 to September 9.
Frequency: As with *Dryas julia*, great numbers were seen in early September, more than half of all observed on September 1, 5 and 7. Hundreds, if not thousands, must have passed unobserved. The majority of this host were faded and torn. Several taken gave out a strong scent of witch hazel, much like that of *Heliconius melpomene*.
Record: 1946—May 28 (3 taken); July 3 (1, 46725), 8 (1, 46752), 30 (200 seen); August 12 (411 seen); September 1 (285 in one hour, all worn), 5 (1 taken, 461134; 463 seen, worn), 7 (700 + seen), 9 (1, 461162). 1948—July 14 (1, 481168), 15 (3 taken, 63 seen), 16 (1), 17 (6 seen), 20 (2), 21 (8 taken, 150 + seen), 24 (1 taken, strong witch hazel scent), 26 (1), 31 (1).

Heliconius procula
(Doubleday and Westwood).

Field Name: Red-hindwing Yellow-banded.

Species Range: Venezuela and Colombia.

Field Characters: With the yellow forewing spots and the solid red hindwing band this species is not distinguishable in flight from *H. clysonimus clysonimus*.

Number: Total recorded, 867. Taken, 22.

Sex: Both sexes taken.

Date: April 29 to September 8.

Frequency: A third species in which large numbers appeared in late July and again in early September. At other times they usually were seen singly.

Condition: Almost all of those seen were in fresh, unfaded condition.

Record: 1946—July 18 (600 + seen), September 8 (3 taken, 461176; 213 seen). 1948—April 29 (1); May 26 (1); June 6 (6); July 6 (1 taken, 6 seen), 7 (1, 481021), 14 (27), 15 (2), 17 (1, km. 30), 18 (1), 27 (2 taken, 26 seen).

Heliconius vibilia vialis (Stichel).

Field Name: Acraeid Mimic.

Species Range: Guatemala to South Brazil and Peru.

Subspecies Range: Guatemala to Colombia.

Field Characters: Hindwing, black-veined striations on orange; with only forewing double (instead of single) band of yellow spots to distinguish it from acraeian species.

Number: Total recorded, 43. Taken, 8.

Sex: Both sexes taken.

Date: April 29 to September 8.

Condition: All specimens fairly fresh.

Record: 1946—September 8 (1, 461143a; 13 seen). 1948—April 29 (1, 481442); May 23 (1 taken, 48545; 3 seen), 26 (1), 31 (1); June 28 (1 taken from flock of 10); July 3 (1, taken, 3 seen), 6 (1 taken, 7 seen).

Heliconius isabella dynastes Felder.

Species Range: Panama to central Brazil and Bolivia.

Subspecies Range: Venezuela.

Field Characters: So exact a mimic of typical ithomiid pattern that it is indistinguishable in life from several species, especially *Mechanitis doryssus veritabilis*, as well as the heliconid *H. anderida holcophorus*.

Number: Total recorded, 7. Taken, 7.

Date: June 17 to July 26.

Condition: All were in good condition.

Record: 1946—July 3 (1, 46725, taken at Pass; 2, 461023, taken at km. 20). 1948—June 17 (1 taken at Pass). July 16 (2 taken), 26 (1 taken).

Heliconius antiochus antiochus (Linnaeus),
form **alba** Riffarth.

Field Name: Four-white-striped Black.

Species Range: Colombia to south Brazil and Peru.

Subspecies Range: Venezuela to south Brazil and Peru.

Field Characters: This black species with its four, forewing, oblique white stripes is unmistakable, except for the rare *aranea* subspecies in which the stripes are yellow.

Number: Total recorded, 228. Taken, 39.

Sex: Both sexes taken.

Date: April 29 to July 27.

Frequency: Decidedly gregarious, occasionally singly.

Condition: Mostly fresh-appearing.

Record: 1946—May 28 (4 taken, 48 seen). 1948—April 29 (1, 48445), 30 (1); May 9 (2 seen), 24 (1, 48583), 28 (1); June 6 (5), 10 (2 taken, 27 seen), 15 (2), 16 (3 taken, 14 seen), 24 (1 taken, 48897; 12 seen), 28 (2 taken, 66 seen); July 5 (3 seen), 9 (3, km. 31), 13 (1 taken, km. 15), 14 (2 taken, 4 seen), 15 (1), 17 (6 seen, km. 30), 19 (2 at Pass, 3 km. 31), 22 (7 seen, km. 35), 23 (pair taken, km. 15), male with strong odor), 27 (1 at Pass, 1 km. 16).

Heliconius antiochus aranea (Fab.).

Field Name: Four-yellow-striped Black.

Species Range: Colombia to south Brazil and Peru.

Subspecies Range: Colombia, Venezuela, Ecuador, Guiana and Amazonia.

Field Characters: This rare species is not to be distinguished from *H. antiochus antiochus* on the wing.

Number: Total recorded, 5. Taken, 2.

Sex: Both sexes taken.

Date: July 8 to 23.

Record: 1948—July 8 (1 taken, 481116), 10 (3 alighted, seen close), 23 (1, 481543).

Heliconius anderida holcophorus Staudinger.

Species Range: Honduras to Colombia and Venezuela.

Subspecies Range: Colombia and Venezuela.

Field Characters: A mimic with typical ithomiid pattern and coloring. Indistinguishable from several species, especially close to *Tithorea harmonia furia*.

Number: A single specimen, a male, taken, May 21, 1948, at Pass. In somewhat worn condition.

Heliconius anderida semiphorus Staudinger.

Species Range: Honduras to Colombia and Venezuela.

Subspecies Range: Colombia and Venezuela.

Field Characters: A large size ithomiid mimic, but with basal half of all four wings rich orange. Indistinguishable in life but closest to *Olyras crathis crathis*.

Number: Only a single specimen, a male, taken, July 15, 1948, at Pass.

Heliconius charithonius (Linnaeus).

Field Name: Zebra-striped Black.

Species Range: North Carolina to Brazil and Peru.

Field Characters: Unmistakable in its

pattern of yellow and black bands across all four wings.
Number: Total recorded, 6. Taken, 3.
Sex: Both sexes taken.
Date: May 24 to July 21.
Record: 1948—May 24 (1, 48584); June 6 (3 seen); July 21 (2).

Heliconius clysonimus clysonimus Latr.

Field Name: Solid Red-hindwing.
Species Range: Costa Rica to Venezuela and Ecuador.
Subspecies Range: Venezuela, Colombia and Ecuador.
Field Characters: Indistinguishable from *H. procula*, otherwise quite distinct.
Number: Total recorded, 90. Taken, 17.
Sex: Both sexes taken.
Date: May 5 to September 8.
Frequency: Usually singly. Only twice seen in any number.
Record: 1946—May 5 (1 taken); September 8 (1, 481177; 39 seen); 1948—May 11 (2 seen), 21 (1), 23 (2); June 6 (2 taken, 12 seen), 10 (15 seen), 18 (1 seen); July 2 (1), 3 (4 seen), 13 (1), 15 (1, km. 15), 17 (1), 21 (1), 23 (2 at Pass, 2 on trail), 25 (1).

Heliconius doris (Linnaeus), form **transiens** Staudinger.

Field Name: Striated-red-hindwing.
Species Range: Colombia and Venezuela to Brazil and Bolivia.
Form Range: Mexico to Colombia and Venezuela.
Field Characters: When flying slowly close at hand or alighted, easy to distinguish from *H. procula* and *H. clysonimus*.
Number: Total recorded, 77. Taken, 8.
Sex: Both sexes taken.
Date: April 29 to September 8.
Record: 1946—September 8 (1 taken, 461175; 10 seen). 1948—April 29 (1, 48453); June 22 (6 seen); July 8 (4 taken, 22 seen), 9 (4 seen), 19 (1 taken, 27 seen), 21 (1, 481540).

form **doris** (Linnaeus).

Field Name: Large Blue-hindwing.
Form Range: Mexico, Colombia and Venezuela to Bolivia and Brazil.
Field Characters: Identical with form *transiens* except for color of hindwing. Of this remarkable mutation-like form only three individuals were observed, although it was striking in appearance and easily identified in its slow flight.
Number: Total recorded, 3. Taken, 1.
Date: July 8 and 10.
Record: 1948—July 8 (1 taken, 481116), 10 (2 seen distinctly).

Heliconius eucoma metallilis Butler.

Field Name: Ithomiid-mimic.
Species Range: Panama to Peru and Amazon Valley.
Subspecies Range: Colombia, Venezuela and Curaçao.
Field Characters: An ithomiid mimic, indistinguishable in flight from several species, as well as from the heliconid *H. antherida holcophorus*.
Number: Total recorded, 36. Taken, 29.
Sex: Both sexes taken.
Date: April 8 to July 26.
Record: 1946—April 8 (1); June 10 (1), 16 (1); July 1 (1), 10 (1), 14 (1), 18 (1), 25 (1). 1948—May 2 (1, 481022), 23 (1, 48573), 28 (1); June 27 (1, 48966); July 2 (1, 481021), 3 (2 taken), 6 (1 taken from group of 4, all alighted), 11 (1, 481148, km. 30), 13 (2 taken), 14 (2 taken), 15 (2 taken from flock of 6), 16 (1), 18 (1, 481248), 26 (3 taken).

Heliconius melpomene (Linnaeus), form **melpomene** (Linnaeus).

Field Name: Red-banded Black Heliconid.
Species Range: Northern South America to Peru and central Brazil.
Field Characters: A common migrant and resident at Rancho Grande. Slow flyer, usually through underbrush and along trails, easily caught with fingers, always giving out a strong scent of witch hazel. In pattern and color very close to the female pierid *Perente charops meridana*, and to the nymphalid *Adelpha lara lara*. In both cases the wings are broader and the flight nervous and swift in comparison with the heliconid. The three species are sometimes seen associated.
Number: Total recorded, 2,566. Taken, 42. Thousands were not counted on days of intensive migration of other species.
Sex: Both sexes taken.
Date: April 29 to September 7.
Note: Never saw them hurrying; often alighting on leaves or blossoms; occasionally courting and mating.
Record: 1946—May 22 (1), 28 (2), 29 (1 taken, 6 seen); August 3 (213 flying slowly through Pass); September 7 (6 seen, 461145; first in a month). 1948—April 29 (1); May 23 (1 taken, 30 seen), 25 (1 taken, 8 seen), 26 (1, 6 seen), 31 (1 taken, 27 seen); June 6 (2 taken, 30 seen), 7 (1, 6 seen), 9 (1, 61 seen), 10 (509 counted and many missed; 4 and 5 males hovering over single female. Many alighted on my sleeves), 11 (18 in twenty minutes), 15 (16 seen), 16 (17 seen), 17 (117 seen), 18 (48 singly, 68 in groups), 19 (2 at 8.30 A.M.), 21 (28 seen), 22 (53 seen), 28 (27 seen, one with nymphalid mimic, flying around each other), 29 (33 seen); July 3 (1 taken, 66 seen), 5 (243 singly or not more than 6 together), 6 (2 taken, 64 seen), 8 (1 soaked in rain, 108 seen), 9 (29 at km. 31 headed for Pass), 10 (66 seen), 11 (4 seen, km. 15), 13 (130 seen, 3 at km. 15), 17 (8 feeding on lantana, km. 30), 21 (368 seen), 29 (1 taken, 66 seen).

Heliconius sara sara (Fab.).

Field Name: Small Blue-hindwing.
Species Range: Panama to south Brazil and Bolivia.

Subspecies Range: Panama, Colombia and Venezuela.

Field Characters: Only to be confused with the very rare *H. doris*, form *doris*, and that hardly, for the latter is a full third larger, although one individual *sara* is unusually large.

Number: Total recorded, 3. Taken, 3.

Date: April 29 to July 25.

Record: 1946—May 29 (1 taken). 1948—April 29 (1, 48445); July 25 (1, 481369).

Philaetria dido (Clerck).

Field Name: Green-spotted Heliconia.

Species Range: Honduras to Peru, Bolivia and southern Brazil.

Field Characters: Only to be confused with the nymphalid *Victorina stelenes*, from which it can be distinguished by much narrower, more elongated wings, and by a slow, wavering flight.

Number: Total recorded, 625. Taken, 4.

Sex: Both sexes taken.

Date: March 15 to September 8.

Frequency: Decidedly gregarious, five large flocks being recorded.

Record: 1946—May 26 (13 passing km. 30), 28 (98 seen), 31 (1 alighted and oriented itself to sun); July 8 (196 seen); September 7 (125 passing slowly but steadily), 8 (250 +, bucking high wind). 1948—March 15 (12 seen); April 15 (16 seen), 29 (1, 48444), 29 (1 taken); June 6 (2 taken); July 15 (1 taken), 21 (1 taken).

1

Neural Adaptations in the Visual Pathway of Certain Heliconiine Butterflies, and Related Forms, to Variations in Wing Coloration[1]

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(Figures 1-8)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The station was founded in 1950 by the Zoological Society's Department of Tropical Research, under Dr. Beebe's direction. It comprises 250 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1800 feet, and the annual rainfall is 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." by William Beebe, Zoologica, 1952, 37 (13) 157-184.

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INTRODUCTION

THE EXPERIMENTS which form the basis of this paper were stimulated by the well-known responsiveness of butterflies to visual stimuli of various colors. Behavioral observations of this phenomenon include those of Eltringham (1933), Ilse (1937). Magnus (1956), and most particularly those of Crane (1955, 1957).

Crane's demonstration of the responsiveness of *Heliconius erato* to orange-red stimuli in feeding and courtship behavior prompted a series of experiments designed to determine the physiological basis of this special sensitivity to long wavelengths. These experiments (Swihart, 1963, 1964, 1965) have demonstrated that: (1) the visual system of *H. erato* includes at least two types of receptors, one maximally sensitive to blue-green and the other peaking in the red (ca. 620 mμ); (2) the receptors interact with each other producing an electroretinogram (ERG) waveform with a distinct color component; (3) specific neural pathways are associated with these receptors. Recordings from the internal chiasma, medulla interna, and the vicinity of the optic nerve demonstrate a spectral sensitivity which indicates a particularly close association between the red receptors and the main pathway of information to the brain.

The behavioral sensitivity of this species seems, therefore, to be related not to any special modification of the receptors, but rather to the development of pathways which "selected" the output from those receptors which transduced information with special biological significance.

The basic hypothesis emanating from these observations was that there was a selective advantage in developing neural mechanisms which demonstrate disproportionate sensitivity to the basic wing coloration, presumably because of the role played by such colors in releasing courtship behavior. This hypothesis invited testing by

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conducting experiments on forms other than *erato,* which possessed different wing coloration, to determine how general this mechanism might be, and the degree of adaptive flexibility afforded by such a system. This paper reports the preliminary results of such a comparative study.

Methods and Materials

Standard electrophysiological techniques were employed. Intact organisms were rigidly mounted with plasticene as previously described (Swihart, 1963, 1964). Evoked potentials were recorded from the optic lobe with a semi-micro (ca. 500 kohm), 3M KCl filled, glass electrode. On the basis of previous experiments (Swihart, 1965), a technique was developed for placing the electrode almost directly into the medulla interna, via a minute hole in the posterior (occiput) region of the head. Usually only very small additional movements of the electrode were required to obtain the long-latency, negative polarity, response characteristic of the medulla interna (see fig. 15, Swihart, 1965).

In order to ascertain that the preparation was continuing to yield "normal" responses to photostimulation, ERGs were recorded simultaneously with a sub-corneal steel electrode. Experiments were terminated if there was any change in the ERG waveform.

Potentials were amplified with Grass P6 D.C. amplifiers, displayed on a Tektronix four beam 564 oscilloscope, and photographed with a Grass C-4 camera for subsequent measurement.

Photostimulation was accomplished with a laboratory constructed stimulator which, automatically, sequentially introduced a series of 15 narrow-band interference filters into an optical system, and provided a 100 msec. stimulus at each wavelength, at a preset and constant interval, usually about one minute. The stimulus duration was chosen as the shortest which would ensure production of all the components of the ERG (Swihart, 1964).

Preparations were aligned so that the stimulating beam, focused by a microscope objective, illuminated nearly an entire eye. The beam axis was perpendicular to the center of the cornea. Histological studies which have been conducted on a number of the forms selected for this study *(Morpho, Agraulis, H. sarae,* and *H. erato),* and physiological experiments involving the stimulation of small portions of the eye (of *H. erato),* have not demonstrated any anatomical or physiological differentiation between various regions of the eye.

Peak transmission points of the interference filters were fairly uniformly spaced throughout the visible spectrum from 404 mμ to 709 mμ. Through the use of a specially-ground, color-compensating filter, and sandwiched gelatin filters, the stimulus energy at each wavelength was held constant ($\pm$ 20%) as determined with an Eppley thermopile.

Equipment was not available for making small, calibrated adjustments in stimulus intensity, hence "spectral sensitivity" (threshold energy) curves were not attempted, rather the electrical magnitude of the response to a standard stimulus of about 5 x 10^3 microwatts/cm^2 was determined.

Spectral efficiency curves were constructed by running through the series of 15 filters three times for each preparation. The magnitude of the response to a particular stimulus was evaluated as a percentage of the largest response to any filter in that particular series. The percentage responses to the three successive series were then averaged to produce the curve for a single preparation. The technique of recording the amplitude of the response, seemed justified since the magnitude of the medulla interna response demonstrates a nearly linear relationship to the log of the intensity of stimulation, within the range of intensities studied. In this range, a tenfold increase in white light intensity, produces an increase in response magnitude of about 30%.

Experimental material was normally captured in the wild and maintained in large outdoor insectaries. This technique permitted the selection and testing of only healthy animals.

Wing spectral reflectance characteristics were measured with a Bausch & Lomb "Spectronic 20" spectrophotometer with reflectance attachment. This equipment measures the reflectance of an area approximately 2 mm x 8 mm. Only specimens which appeared to be newly emerged were used for such determinations.

It will doubtlessly be noted that the number of specimens of each species investigated is frequently very small. It is hoped that this will be understood as related to certain problems which were encountered, including: (1) the physical difficulty of capturing healthy specimens of certain elusive and rare species, notably *Philaethria* and *Morpho;* (2) the extremely delicate nature of these organisms which results in their entering a state of "shock" if handled roughly. This condition is evidenced by abnormal behavior, including strong positive phototaxis, and highly aberrant evoked potentials, usually accompanied by very large (ca. 5 mV) low-frequency spontaneous discharges; (3) the necessity of limiting the observations to only those individuals which produced strong "day" type electroretinograms (Swihart, 1963); (4) the problems in placing the micro-electrode into the intact organism in such a manner that it reaches the very limited region near the medulla interna, which yields the long-latency negative potentials, without inducing operative trauma, and its resultant massive spontaneous activity.

Six species of butterflies were selected for this study. All belong to the family Nymphalidae. Four are members of the subfamily Heliconiinae, while the Morphinae is represented by one form *(Morpho)*, and the Nymphalinae by *Victorina.*

Studies were begun on *Heliconius sarae* because of its fairly close relationship with the subject of previous experiments, *H. erato*. In Trinidad, *erato* is a small black butterfly (2½" wingspread) with bright red spots on the forewings. *H. sarae* is, in many respects, a very similar butterfly, with the most obvious difference being the substitution of a pair of bright yellow bands on each forewing. In addition there is a moderately strong blue irridescence on the hind wings.

Heliconius ricini was chosen because it offered an "intermediate" color pattern to *sarae* and *erato*. In *ricini,* the black "base" color of the wings is broken by forewing yellow bands (as in *sarae*), but a large red hindwing spot is also present. *H. sarae* and *ricini* are the most closely related of the forms tested. Both belong to the same species-group as discussed by Emsley (1965).

The third form chosen, *Agraulis vanillae,* was selected because its color pattern is similar to that of a number of other primitive Heliconiinae. That is to say, the wings are predominantly bright orange in color.

Even a cursory glance at the variety of wing color patterns characteristic of the Heliconiinae demonstrates a single basic plan. This is a long-wavelength color with a contrasting dark brown or black. It can be seen that the aforementioned forms are representative of this basic pattern. However, for purposes of investigating the physiological adaptations of the visual pathway, it seemed desirable to investigate forms with an unusual wing coloration. Initially, it was hoped that studies could be made on the rare, predominantly green heliconiine, *Philaethria dido;* however, only a single healthy specimen of this species was obtained, and observations were extended to the very similarly marked nymphalid, *Victorina steneles.*

Finally, to further extend the variety of wing colors, observations were made on the blue-winged *Morpho peleides.*

The results of the observations on each species will be considered separately.

Results

Heliconius sarae thamar Hubner

A total of eight individuals that were tested yielded acceptable responses, i.e., long-latency negative potentials. A ninth individual producing such responses became erratic before the experiment was completed; however, its performance in the early stages of the experiment gave a clear indication of its sensitivity.

It was found that the spectral efficiency curves produced by these individuals were far from being identical to each other. Examination of the curves revealed that they could be separated into two distinct types, with each category being fairly homogeneous. Figures 1 and 2 show these two types of curves. Four individuals demonstrated a sensitivity peak in the orange-red portion of the spectrum (ca. 620 mμ); the remainder were maximally sensitive to green.

In spite of the small sample size, the differences between these two curves is so great that there is no statistical basis for doubting that they represent two distinct populations. Thus, for example, one obtains by comparing the percentage responses at a single wavelength (523 mμ), at value of 4.78, with a $n = 7$*. The probability that the responses represent different populations is thus greater than 0.995. If this analysis is carried to additional points on the spectra, no reasonable doubt can remain.

The red-sensitive curve peaks at 620 mμ, and in this respect is very much like the responses recorded from *erato*. However, there is a difference between the two forms in their sensitivity to shorter wavelengths. Thus, the response of *sarae* to stimulation with short wavelengths is, on the average, considerably greater than *erato* (Fig. 2).

Figure 3 shows the spectral reflectance curves of the *erato* red pigment, and the *sarae* yellow. It can be seen that the yellow color could actually be described as "blue negative," since it actually reflects about the same amount of red as does the *erato* pigment. If one, therefore, considers the difference between these colors in terms of a greater reflectance of mid and shorter wavelengths, there is a parallel in the differences between the reflectance and spectral efficiency curves in the two forms.

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* where

$$n = \frac{\left(\frac{s_1^2}{N_1} + \frac{s_2^2}{N_2}\right)^2}{\left(\frac{s_1^2}{N_1}\right)^2 \frac{1}{N_1+1} + \left(\frac{s_2^2}{N_2}\right)^2 \frac{1}{N_2+1}} - 2$$

which is an approximation of a longer formula given by Welch (1947).

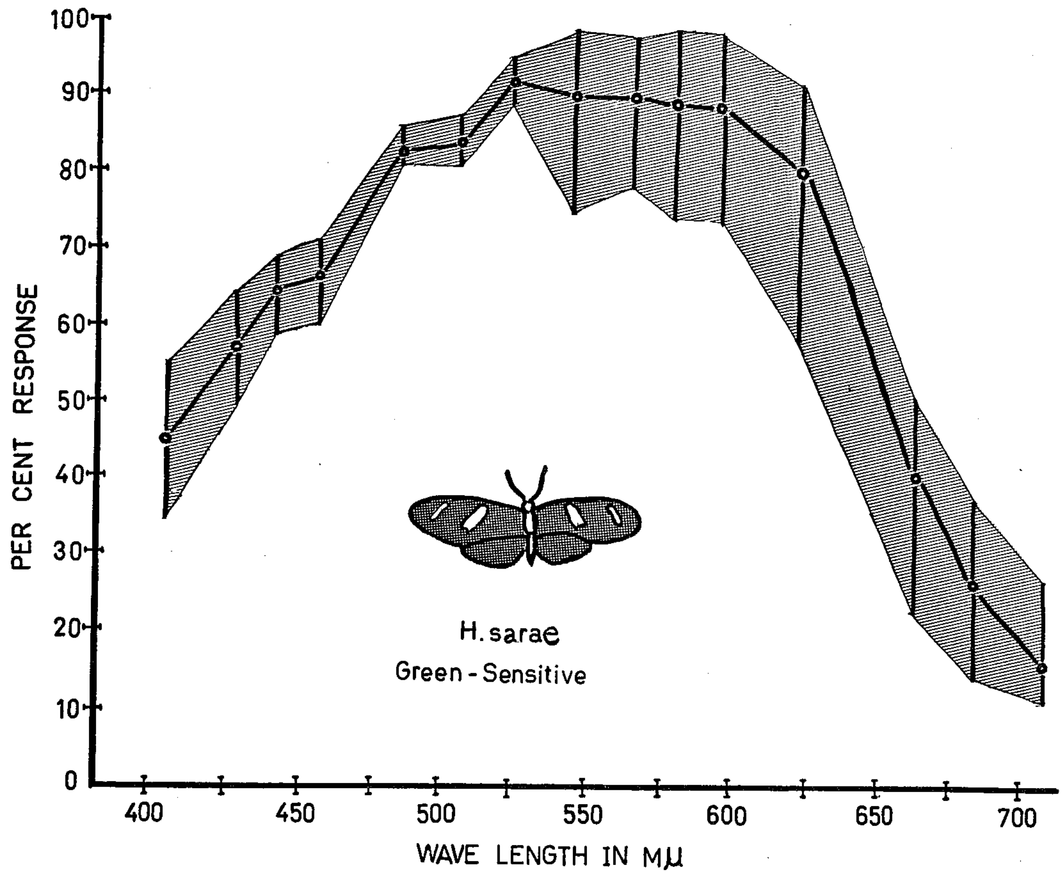

FIGURE 1.
One of the two types of spectral efficiency curves found to be characteristic of *Heliconius sarae.* Measurements were based upon the magnitude of long-latency, summated potentials of negative polarity in the vicinity of the medulla interna. See text for details of technique. Vertical bars indicate the limits of observed variability between individuals, i.e., the maximum and minimum responses to any given wavelength. Illustration is a semi-diagramatic representation of the dorsal surface; unshaded portions correspond to the areas of yellow pigmentation. Shaded area represents the distribution of near black wing pigmentation. Unless otherwise noted, all subsequent diagrams are to the same scale.

The other type of spectral efficiency curve was recorded with the same frequency as the red-sensitive one (four of each, with the previously mentioned ninth being red sensitive). It would appear that the sensitivity of these organisms was largely determined by the green-sensitive receptor system with a slight and variable skew produced by the presence of the red system.

At this time it is impossible to identify the factors which contribute to the differences between these two types of individuals. All the organisms were tested at approximately the same time of day (late morning), and demonstrated similar "day" type electroretinograms. Three males and one female yielded the red-sensitive curve, while three females and one male produced the green curve. The age of the individuals was not known since they were all wild caught specimens.

It should be remembered, however, that behavioral observations on butterflies have demonstrated rather dramatic shifts in the colors to which they will respond, depending upon their physiological state. Thus, Ilse (1937) showed that while *Pieris brassicae* selected red, yellow or blue colors in its feeding behavior, it became specially responsive to the color green when involved in egg-laying behavior. It may well be that such shifts in spectral sensitivity represent a measurable index of the rather abstract concept of "physiological state."

Heliconius ricini (L.)

A total of eight specimens of this species pro-

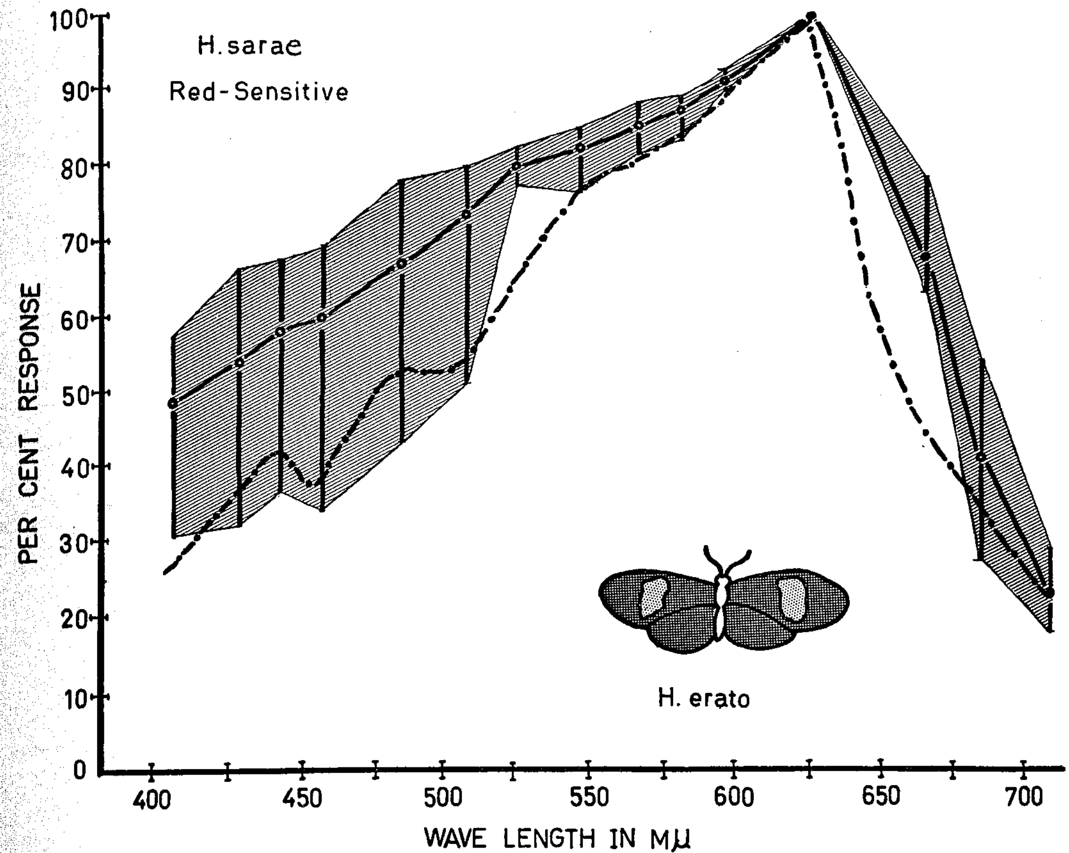

FIGURE 2.
Alternate type of spectral efficiency curve that may be recorded from *Heliconius sarae* which demonstrates far greater sensitivity to long wavelengths than does the curve in Figure 1. Also included in the figure, for purposes of comparison, is the comparable average spectral efficiency curve recorded from four individuals of the species *Heliconius erato* (dot-dash-line). Also figured is the distribution of red pigmention in the forewings of *H. erato.*

duced acceptable responses. In spite of the fact that the wing coloration of this form can be considered to be intermediate between *sarae* and *erato* (i.e., has both red and yellow markings), the responses were entirely similar to *sarae.* Thus three of the individuals yielded spectra peaking in the red (Fig. 4) (620 mμ), with no significant differences from the *sarae* red-sensitive curve. One of the specimens tested was most interesting in that the nature of its response changed during the course of the experiments. The responses to the initial filter series indicated a maximum sensitivity to red. A gradual change took place, without any apparent change in the waveform of the response, so that by the time the organism was stimulated by a fourth series of filters, the response was plainly maximally sensitive to green light.

The remainder of the organisms tested produced the non-specific green-sensitive curve.

Agraulis vanillae vanillae (L.)

Five specimens of this primarily orange-colored butterfly produced acceptable responses. The averaged responses of these individuals produced a curve which is distinctively different from any which had been previously recorded (Fig. 5). In many respects, this spectrum can be considered to be entirely intermediate between the two *sarae* spectra. Thus, *Agraulis* demonstrates a curve peaking in the orange, less sensitivity to short wavelengths than the *sarae* green curve, and less sensitivity to long wavelengths than the *sarae* red curve. These differences are so great that there is little or no overlap of even those responses demonstrating the

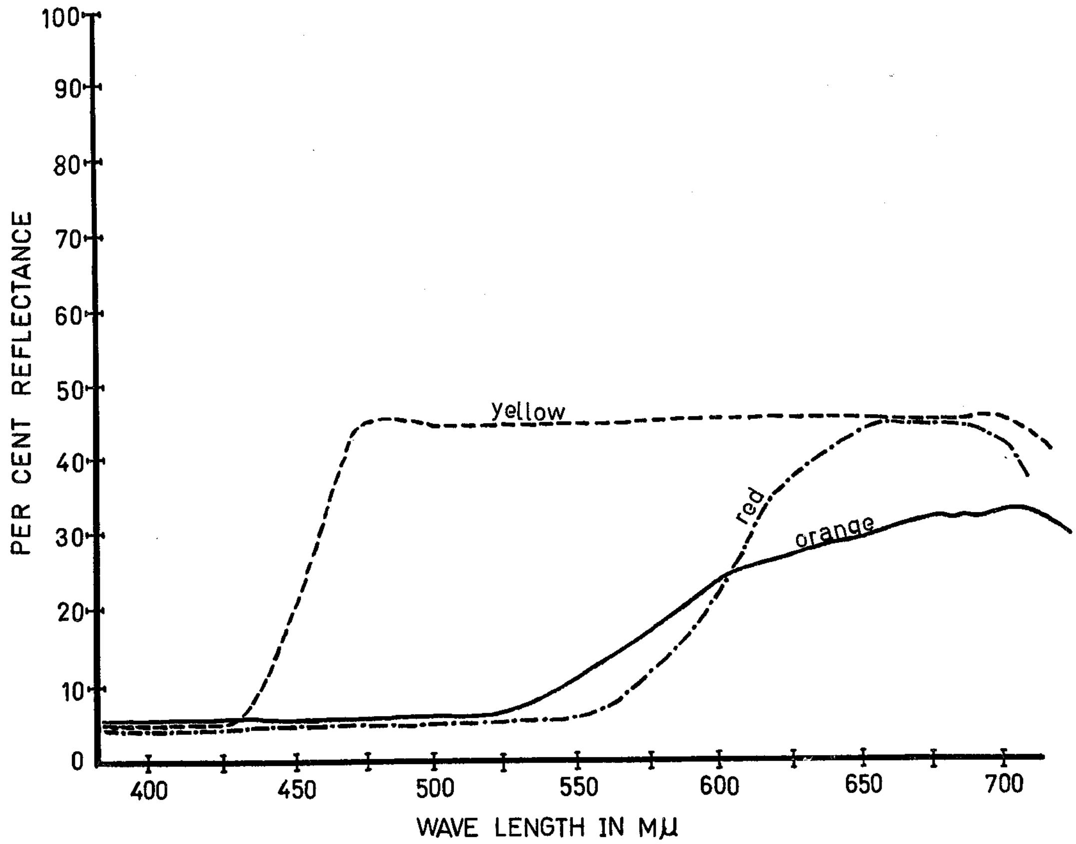

FIGURE 3.
Spectral reflectance characteristics of various heliconiine wing pigments as measured against a magnesium carbonate standard. Intact wings were mounted on a nonreflective backing before being inserted into the spectrophotometer. No differences in reflectance exist between similar appearing areas in the various species, e.g., *erato* and *ricini* red are identical.

greatest variance from the mean in most of the aforementioned portions of the spectrum.

It will be noted that, like *erato,* only a single type of response was recorded from this species.

Philaethria dido dido Clerck and *Victorina steneles* (L.)

It was hoped that observations could be made on the green-winged heliconiine *Philaethria* as it would provide a form with a markedly different wing coloration. Unfortunately, not a single wild specimen could be obtained. Several eggs were located, however, and a single healthy specimen was raised in the laboratory. Testing of this individual did indeed produce responses showing a distinctive peak in the green. Regrettably, no additional specimens were available to confirm these observations. Because of the shortage of *Philaethria,* it was decided to make observations on the remarkably similar nymphalid *Victorina.* These forms are so similar that they can be easily confused. The resemblance is much more profound than mere superficial appearance. Both forms have developed their green coloration by a most interesting technique. In the green areas of the wings, the scales are either much reduced, or missing, and the pigmentation is within the wing membranes. The coloration itself appears to be due to the presence of two pigments. One of these absorbs in the blue (i.e., appears yellow) and can be extracted with ether, leaving an insoluble blue compound behind (Fig. 6). It seems likely that this unusual wing coloration is due to haemolymph pigments (Hackman, 1952) since *Victorina*'s blood and eggs are both bright grass-green.

Four specimens of *Victorina* were tested and found to resemble *Philaethria* in visual mechanisms as well as in pigmentation. Figure 7 shows

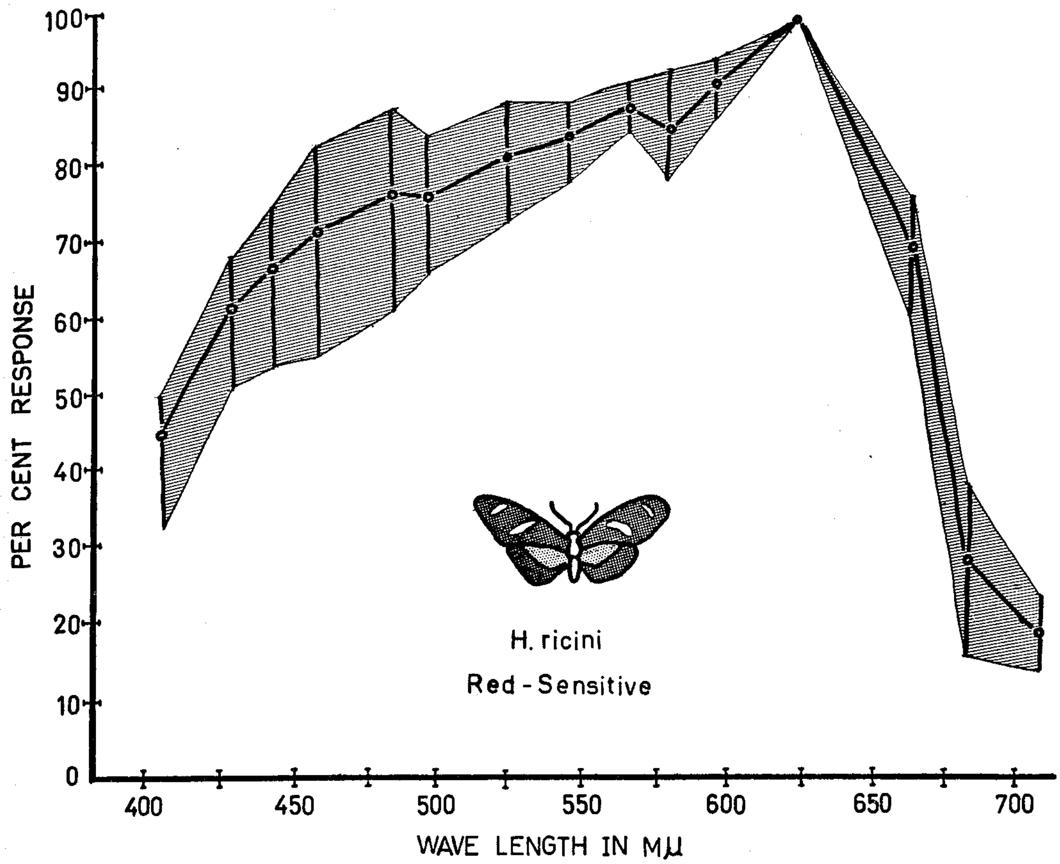

FIGURE 4.
One of the two spectral efficiency curves characteristic of *Heliconius ricini.* Note the great similarity to Figure 2. The other type of curve is similar to the *sarae* "green-sensitive" curve illustrated in Figure 1. Unshaded areas of illustration correspond to the distribution of the yellow pigment, while the lightly shaded area represents the hind-wing red spots.

the luminosity curve produced by these individuals which clearly peaks at about 565 mμ. There can be no doubt that this curve is distinctly different from the green-sensitive curve of *sarae*. At virtually every wavelength longer than the 565 mμ maximum, the *Victorina* responses are so greatly reduced that there is very little, if any, overlap with even those *sarae* showing the greatest deviation from the mean.

The curve recorded from the single *Philaethria* was entirely similar to that produced by *Victorina,* and fell well within the limits of *Victorina* variability.

Morpho peleides insularis Fruhstorfer

It was considered advisable to make tests on a form with a primarily blue wing coloration. Since there is no such heliconiine in Trinidad, it was decided to utilize the large blue-violet morphine *Morpho peleides*. This butterfly is well known to show a special sensitivity to the color blue. For many years, professional collectors have used this fact to assist in the capture of this elusive species, with its highly prized iridescent physical coloration.

Two specimens of this species were fully tested for spectral efficiency. The electrical responses produced by these organisms were found to be so different from the responses of the heliconiine that direct comparison is difficult. The electroretinograms show none of the complexities, described in detail for *erato* (Swihart, 1964). The waveform consists of a B wave, followed by a uniform, sustained negativity during illumination. All the ERG components usually associated with the red-sensitive receptor, such as the "dip" following the B wave, and "off" effect, are totally absent.

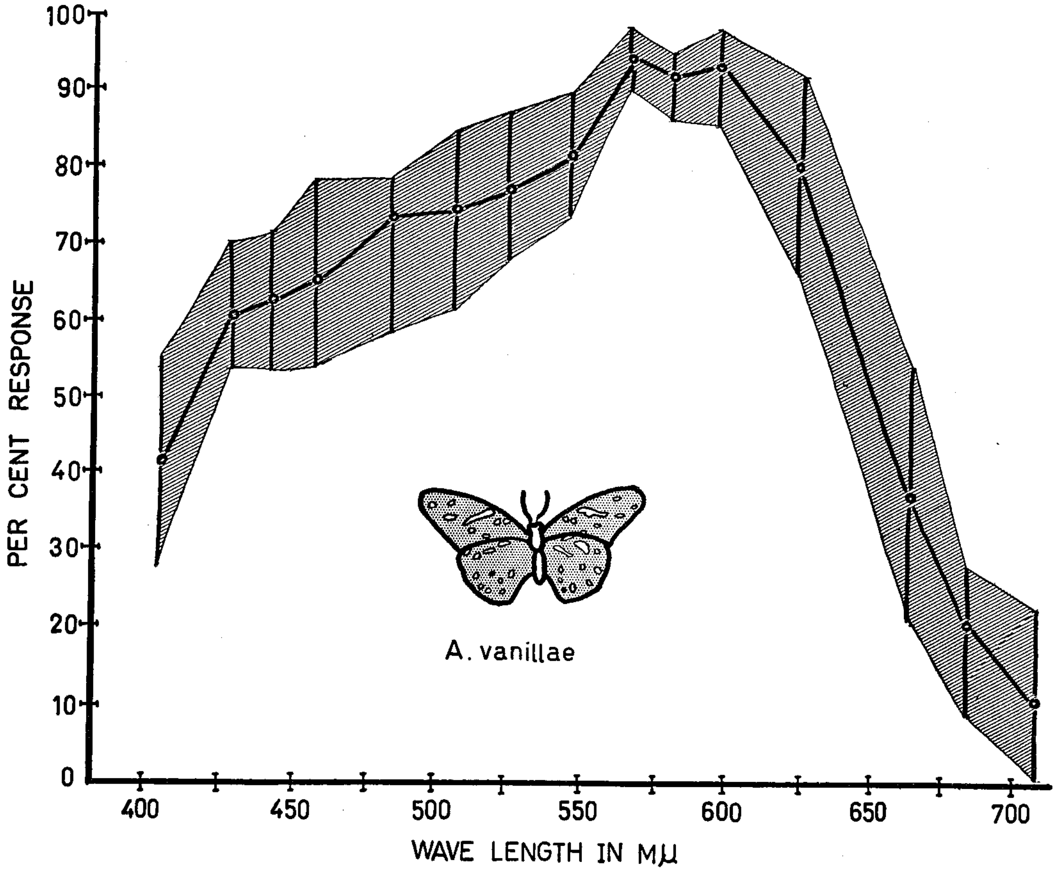

FIGURE 5.
Single type of spectral efficiency curve recorded from five specimens of *Agraulis vanillae*. This species is a nearly uniform orange color (light shading), with numerous small black (unshaded) spots on the wings.

These differences in the ERG waveform are reflected in differences in evoked potentials, as recorded with micro-electrodes. Unlike the heliconiine, it was found that the evoked potentials were generally directly proportional in magnitude to the size of the ERG. The spectral efficiency of these effects, as measured by the ERG B wave magnitude, is indicated by Figure 8. The skew of this curve towards the blue, with its peak at about 485 mμ is both obvious and strikingly different from the curves produced by the heliconiine.

Two additional specimens of this species were tested in the course of work preliminary to the experiments which form the basis of this report. Full spectral efficiency curves, as determined by the standard technique, were not calculated for these individuals. They did, however, appear to demonstrate the same ERG waveform and great sensitivity to short wavelengths.

Discussion

It is unfortunately true that the fundamental mechanisms of color vision remain largely unexplained. This lack of knowledge is particularly apparent in the case of invertebrates, where even the method of coding color information has not been identified as has been done for certain vertebrates (e.g., Wagner *et al.*, 1960; Muntz, 1962).

Recent microelectrode studies (e.g., Horridge *et al.*, 1965) have revealed a vast complexity in discharge patterns in the insect visual pathway. There is, however, some question as to the adequecy of such single fiber techniques to record from those fibers most intimately involved in the highest forms of behavior. There can be no doubt that these techniques tend to select large-diameter fibers. Such neurons have been repeatedly demonstrated to be associated with flight or escape reactions, and hence can hardly be

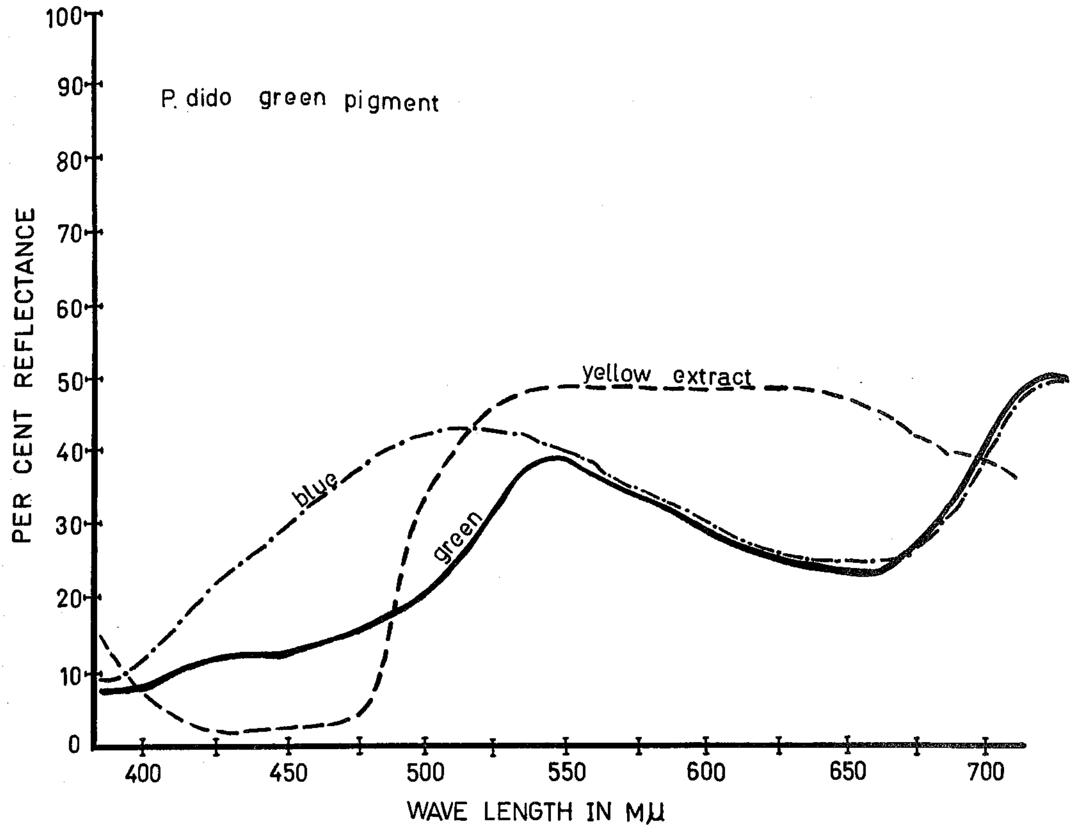

FIGURE 6.
Reflectance characteristics of the green wing areas of *Philaethria dido* and *Victorina steneles*. Since the scales are much reduced, or absent in these regions, they are quite translucent and reflect poorly. Because of this fact, the wing reflectance was measured with a white backing. This technique increased the height of the curve without altering its shape. Solid line illustrates the characteristics of the natural wing coloration. Dot-dashed line indicates the reflectance of the wings after being extracted with ether. Dashed line indicates the transmittance of the yellow-colored extract. The height of this curve was adjusted by plotting $\frac{\%\ \text{transmittance.}}{2}$

considered as representative. For these reasons semi-microelectrodes have been employed in the current study, as it seems not unlikely that a "summated" response reflects the nature of the nervous activity with somewhat less bias.

In this connection, it should be remembered that it was demonstrated (Swihart, 1965) that there are fibers with discharge patterns related to the magnitude of such summated potentials. Thus, the curves presented in this report reflect the discharge frequency (and hence the total number of spikes per stimulus of standard duration) of at least some of the neurons in the visual pathway.

Recently, Goldsmith (1965) has given evidence that spectral sensitivity curves derived from summated (ERG) potentials must be carefully interpreted if screening pigments are present. Such problems are not encountered in the genus *Heliconius,* where the only pigmentation appears to be a nearly black substance, localized in granules within the iris pigment cells.

In the case of *Agraulis* and *Victorina* there is a light orangish pigmentation within the corneal cuticular layer. This pigmentation does not appear to penetrate to the deeper layers of the eye, and hence probably could not produce the effects described for *Musca.* However, the role of such accessory pigments deserves further investigation.

A careful analysis of the techniques employed in these experiments may suggest that they lack

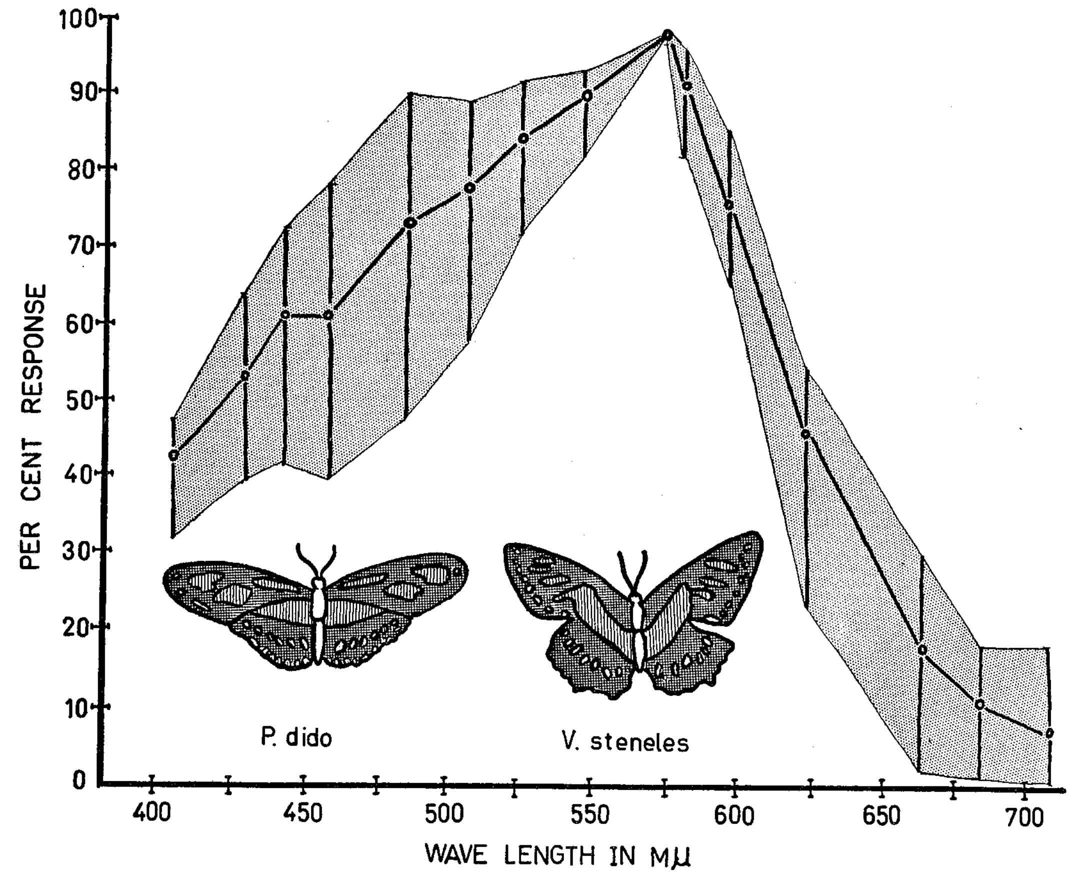

FIGURE 7.
Spectral efficiency curve recorded from four specimens of *Victorina steneles*. The single specimen of *Philaethria dido* demonstrated a similar sensitivity. Lightly shaded areas of illustration represent the distribution of the green coloration, as opposed to the dark brown-blackish pigmentation.

some of the controls commonly employed in the investigation of primary visual events. It must be remembered that this is primarily a comparative study and that the techniques employed on one form were identical to those used on the others. Thus, while it may not be possible to interpret the results as representative of photopigment absorption spectra, they are indicative of real differences which exist between closely related forms.

It is reasonable to enquire as to the origin of these differences.

Analysis of the magnitude of the electroretinograms, in a method analagous to that described in this paper, produces spectral efficiency curves with no significant differences between the various Heliconiinae. In every case the curves resembled that described for *H. erato* (Swihart, 1963). This fact strongly suggests that the variations between forms cannot be related to differences in the nature of the photopigments.

Alternatively one might suggest that the variations in sensitivity are due to differences in the relative numbers of several different types of receptors, (e.g., *Calliphora;* Autrum & Burkhardt, 1961). However, an explanation based upon such a rigid mechanism seems inconsistent with the type of variability observed in *sarae* and *ricini.*

For such reasons, it seems most reasonable to interpret the observed variations in the summated responses to various colors, as a neural phenomenon.

Turning to a consideration of the spectral efficiency curves themselves, we find a most interesting series in the responses of *Agraulis, sarae* and *erato.* In considering these forms, it is worth noting that casual behavioral observations

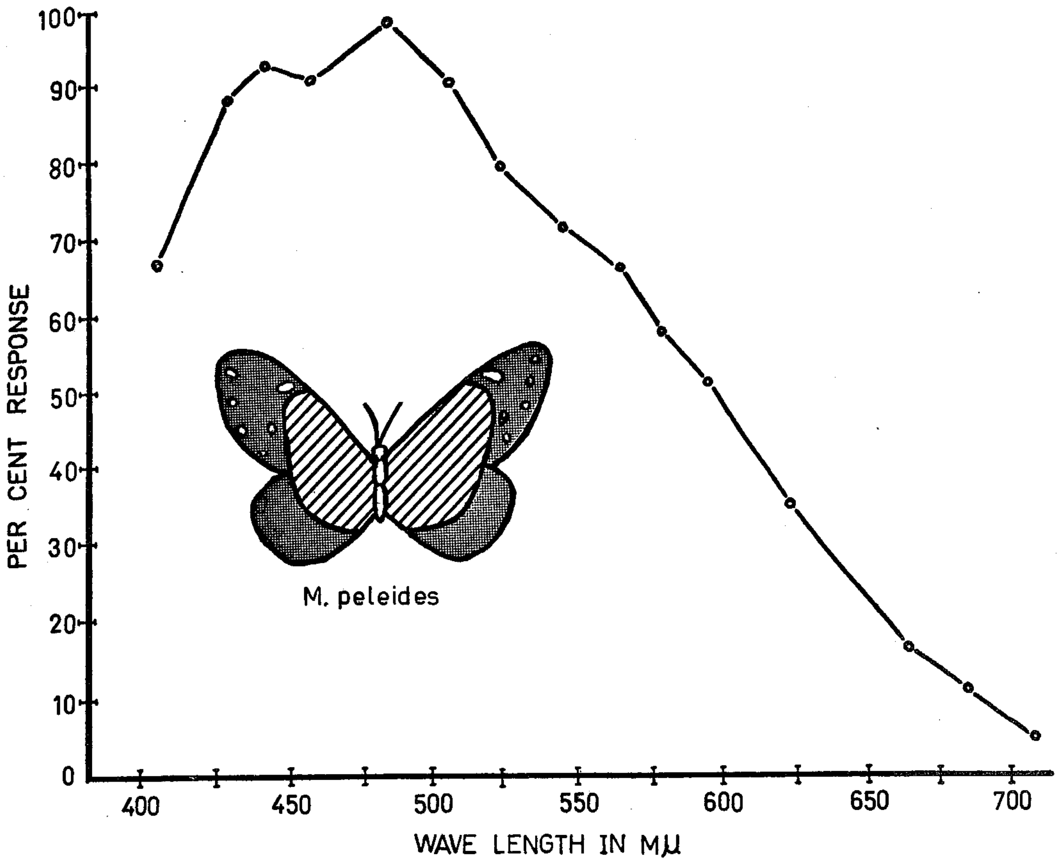

FIGURE 8.
Average spectral efficiency curve derived from two specimens of *Morpho peleides*, as determined by the ERG B-wave magnitude. Very little variability between the individuals was observed. Illustration is at reduced scale. Central (hatched) areas of wings is iridescent blue, with contrasting brown-black margins.

by the author have indicated that consistently stronger behavioral responses to specific colors are produced by the species with the red and orange markings. In the case of *sarae*, attempts to demonstrate a behavioral sensitivity to yellow or red have, as of this time, produced no positive responses in courtship (Crane, pers. com.). This condition would seem to have a physiological correlate in the existence of the two types of spectral efficiency curves recorded from this form, as opposed to the uniformity which characterizes the two other species.

It would appear that considerable significance can be attached to the variability between individuals producing each of the two different *sarae* curves. Each of the curves demonstrates a highly asymmetric distribution of the degree of variability, which would hardly be expected on the basis of a "normal" distribution of variance. The most likely interpretation of these curves would seem to be that the green-sensitive curve reflects the activity of a visual system responding primarily to the sensitivity of a blue-green sensitive receptor, with a small and variable contribution by a red-sensitive system. On the basis of such an interpretation, the short wavelength portion of this curve (400-525 mμ) would probably reflect a portion of the inherent sensitivity of the receptor system. Conversely, the red-sensitive curve illustrates a high degree of variability only at wavelengths below 525 mμ. This would seem to imply that the system is responding primarily to a red-sensitive receptor (maximum 620 mμ), with a small and variable contribution by the blue-green system. These two maxima observed in *sarae* are the same as those reported for *erato* (Swihart, 1964).

By comparison, the single type of spectral efficiency curve characteristic of *Agraulis* demonstrates a fairly uniform variability throughout the spectrum. This would seem to indicate that the mechanism is not "dominated" by a single receptor system, but rather reflects the neural summation of the activity in several receptor types. Indeed, the peak of such a curve may not correspond to any specific type of receptor, but, rather, indicate a region where the overlapping sensitivity of two receptors "summates" to produce an "artificial" peak. It is, therefore, interesting to note that the peak of the *Agraulis* curve lies midway between the maxima of the two receptors postulated for *sarae* and *erato.*

Extending our analysis to the other forms studied, we find that *ricini* is similar in all respects to *sarae.* This is not particularly surprising when one considers both the extremely close phylogenetic relationship between the two forms (Emsley, 1965) and the basically similar wing coloration (i.e., forewing yellow bands).

Turning to the two similar green forms, *Philaethria dido* and *Victorina steneles,* we find several significant differences from the species previously considered. First is the rather obvious shift in the peak from the 528 mμ region to about 570 mμ. The very small variance between individuals at the peak of the curve suggests that this is probably due to a difference in receptors rather than a mechanism such as that postulated for *Agraulis.*

The second remarkable feature of the *Victorina* curve is the extremely attenuated response to long wavelengths. It seems most unlikely that the orange color of the cornea could be responsible for the diminished responsiveness to long wavelengths. While it is possible that this portion of the curve represents the sensitivity of the receptors, it seems much more probable that some other mechanism is involved (e.g., inhibition by a red receptor system).

It is difficult to extend the preceding type of analysis to *Morpho,* since the responses of this form (ERG and neural) are so different from the preceding forms as to make a direct comparison difficult, if not impossible. Regardless of the final interpretation of the nature of the visual mechanisms of this form, it is clear that virtually all the recorded responses demonstrate a maximum sensitivity to the blue portion of the spectrum. It is obvious that this organism must possess a blue-sensitive receptor. The question is, therefore, whether this represents a unique type of receptor. The neural responses of the other forms have given but little indication of any special sensitivity to short wavelengths. Only *Victorina's* neural spectral efficiency curve demonstrates the type of variability between individuals which could be interpreted as being clearly indicative of the activity of a blue sensitive system. On the other hand, spectral efficiency curves based upon the ERG B-wave demonstrate a rather considerable sensitivity to short wavelengths. This is true even in the case of the primarily red-sensitive *erato* (Swihart, 1963). It seems possible, therefore, that such a system may be fairly commonly distributed among the Nymphalids; however, evolutionary adaptation has resulted in its contributing little or nothing to the excitation of the information pathway in the vast majority of species where the primary wing coloration is in the long wavelength portion of the spectrum.

To conclude this discussion, it is interesting to speculate as to the evolutionary forces which have contributed to the development of the weak and variable responses characteristic of the forms with the yellow forewing bands, i.e., *sarae* and *ricini.* In considering this problem, one must remember that there are two important factors which have played a role in the development of butterfly wing coloration. These are: protective (warning or mimetic) coloration and the conservative force of sexual selection. These two forces are frequently antagonistic. In fact, the opposing pressures of these two factors are believed (Brower, 1963) to have produced the multiple cases of sexual dimorphism in wing coloration found in butterflies.

As previously noted, many of the primitive Heliconiinae are primarily orange in color. This coloration appears to be due to a pterin pigment (Baust, 1967). A small modification of this molecule has produced the erythropterin pigmentation found in the red spots of *erato,* etc. It seems not unlikely that this refinement of the chromophore, which has produced a coloration with greater purity, has allowed the refinement of highly specific behavior patterns based upon the releasing value of this striking color.

On the other hand, the yellow pigmentation of *sarae* and *ricini* represents the development of an entirely new type of pigment (an amino acid, Brown, 1965) probably in response to some other pressure. It is certain that these forms have not lost the ability to synthesize a pterin pigment since almost all the Heliconiinae demonstrate minute red spots at the base of the forewing. Employment of the yellow pigment vice the red is hard to explain in terms of sexual selection since the low color purity of this pigment would make an inherently poor sign stimulus. On the other hand, the yellow reflects about 207% more light in the visible spectrum than does the red. It seems certain this more brilliant pigmentation is considerably more effective as warning coloration. The species has had to accommodate to this increased emphasis on warning coloration with a lessened dependence on wing coloration as a courtship releaser. This change appears to be reflected in the less specific neural adaptation of the visual pathway to the organism's wing coloration.

It must be admitted that many of the ideas which have been put forth must remain in the category of speculation. To some extent, this seems to be an inherent penalty for attempting to penetrate the perceptual world of another species.

Summary

Specimens of six species of butterflies were examined using standard electrophysiological techniques. Spectral efficiency curves were constructed for each species. For five of the species, this was done on the basis of the magnitude of long-latency, negative polarity, summated potentials, associated with the activity of higher order neurons in the vicinity of the medulla interna.

Two species with yellow forewing spots (*Heliconius sarae* and *H. ricini*) produced similar results, i.e., individuals yielded one of two types of curves, one a non-specific curve peaking in the green, and another peaking in the red, with a shape very similar to the spectral reflectance of the yellow wing pigmentation. The orange butterfly, *Agraulis vanillae,* produced a single type of curve peaking in the orange. The two green butterflies, *Philaethria dido* and *Victorina steneles,* produced curves peaking in the green. The blue butterfly, *Morpho peleides,* produced very different electrical responses. The electroretinogram did not demonstrate the components, which in the preceding forms, are associated with a red-receptor system. The spectral efficiency curve based upon *Morpho*'s ERG B-wave demonstrated a maximum in the blue.

On the basis of these observations, and previous studies of a form with red markings *(Heliconius erato),* it is suggested that butterflies possess a neural mechanism which "selects" the output from various receptors in such a manner so as to make the visual system respond maximally to stimulation with colors approximating the wing pigmentation.

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