THE INHERITANCE OF HINDWING DISCAL SPOT COLOR IN *COLIAS PHILODICE*

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Instances of sustained conspicuous variation among the individuals of a single interbreeding population are of special interest to evolutionary biologists. FORD (1953) has recently reviewed the state of knowledge of this "balanced polymorphism" in the Lepidoptera. The conspicuous variability in species of the genus *Colias*, especially in North America, is familiar to butterfly collectors but has been confusing and often controversial. Some of the sympatric variation in *Colias* is due to natural interspecific hybridization or to environmental effects, but there are certain characters which vary within each species and which are controlled by one or a few pairs of genes. The most familiar is the ground-color of the female, in which the "alba" form is produced by a dominant sex-limited gene and colored females are homozygous for the recessive allele. I have summarized our knowledge of genes and polymorphism in *Colias* elsewhere (Remington, 1954).

The color of the discal spot on the upperside of the hindwing has received very little attention, although its great variability in some species has been known for a long time. Every species of *Colias* and its near relative *Zerene* has the hindwing discal spot. In the orange species it is rather uniformly orange or orange-red except in "alba" females, where polymorphism is then visible (*e.g., C. eurytheme* Bdv. and *C. lesbia* Fab.). Some yellow species have the spot consistently pale yellow (*e.g., C. palæno* L.) or occasionally have an orange-tinted spot (*C. alexandra* Edw., *C. scudderi* Reak., *C. behrii* Edw.). However, *C. philodice* Latr. and some other yellow species show marked polymorphism in most or all populations; individuals having the spot pale yellow fly with others having the spot deep orange, and the intermediate grades of color occur at the same time.

During our studies at Yale of *Colias* genetics, we have reared a number of broods of *C. philodice* from Connecticut which give some evidence of the inheritance of the color of the spot. The arrival of the J. H. GEROULD COLLECTION at Yale has permitted the analysis of additional broods of *C. philodice* from New Hampshire. These are included in the table. Other work made it not feasible to take the time required to make a photometric analysis with precise instruments, and an arbitrary color standard was established, with an index series of specimens for frequent reference. The palest spot, with no orange or red scales, was designated "yellow." The reddest spot (near "Orange Chrome" of Ridgway, 1912) was called "orange." Three evenly spaced grades between "yellow" and "orange" were designated "pale semi-orange," "semi-orange," and "deep semi-orange."

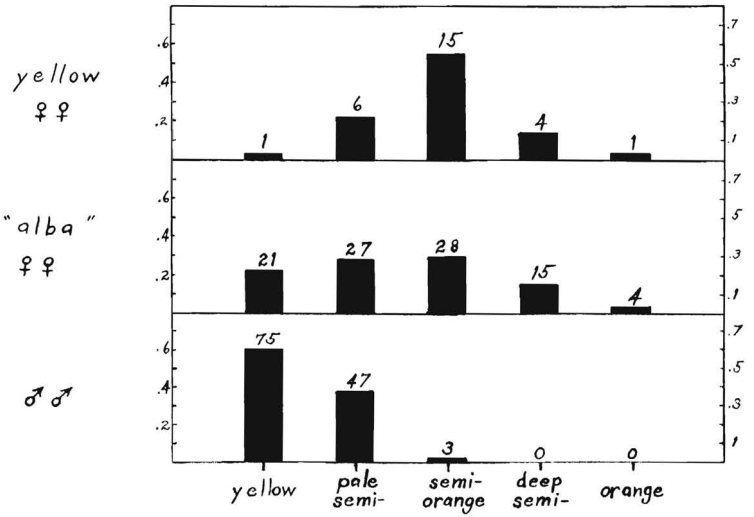
One of the first discoveries was the difference between the spot colors in males, "alba" females, and yellow females. The figure shows graphically the fact that the discal spot is much paler in males than in females having es-

Table of hindwing discal spot color in Connecticut (58 to 75A-D) and New Hampshire (1909a to 1920ι) broods of *Colias philodice.**

Brood No.	♀ Parent	♂ Parent	F_1 Offspring				
			yellow	pale semi-	semi-orange	deep semi-	orange
58	*aa* deep semi-	? (wild)	0-0-0	4-0-1	15-0-25	4-0-7	0-0-0
58H	*aa* semi-or.	semi-or.	0-0-0	1-0-0	7-0-2	0-0-0	0-0-0
62C	*aa* orange	pale semi-	0-0-0	2-0-0	11-0-4	0-0-3	0-0-0
70B	*aa* semi-or.	yellow	4-0-0	2-0-1	0-0-1	0-0-0	0-0-0
70B-A	*aa* pale semi-	pale semi-	5-0-0	5-2-3	2-7-5	1-0-5	0-0-0
75A	*Aa* pale semi-	same ♂ (70B-A)	12-1-0	1-3-2	13-9-11	1-0-5	0-0-0
75A-C	*Aa* semi-or.	yellow	9-0-0	0-3-1	0-2-4	0-0-0	0-0-0
75A-D	*aa* semi-or.	semi-or.	0-0-0	2-0-0	3-0-3	1-0-0	0-0-0
1909a	*Aa* semi-or.	? (wild)	5-0-0	21-3-2	10-3-9	0-0-4	0-0-0
1909w	*Aa* deep semi-	semi-or.	0-0-0	6-3-1	10-2-1	1-2-0	0-0-0
1910g	*Aa* semi-or.	? (wild)	52-14-6	4-11-10	0-7-4	0-3-1	1-0-0
1910i	*aa* (lost)	yellow	27-16-6	2-13-6	0-2-2	0-0-0	0-0-0
1910k	*aa* semi-or.	yellow	29-6-3	4-4-5	0-5-7	0-1-0	0-0-0
1910b	*Aa* deep semi-	? (wild)	4-0-0	18-4-2	42-13-15	7-4-5	0-0-0
1910o	*Aa* semi-or.	semi-or.	0-0-0	2-1-0	4-2-3	1-0-1	0-0-0
1910e	*aa* deep semi-	pale semi-	7-3-2	35-4-6	12-4-4	0-0-1	0-0-0
1910f	*aa* semi-or.	pale semi-	1-2-0	8-2-2	1-3-3	0-0-0	0-0-0
1920ι	*Aa* semi-or.	pale semi-	75-21-1	47-27-6	3-28-15	0-15-4	0-4-1

*Hyphenated figures show in order the number of ♂♂, of "alba" ♀♀, and of yellow (*aa*) ♀♀; thus, Brood 1910g produced 52 ♂♂, 14 "alba" ♀♀, 6 yellow ♀♀ with the discal spot yellow. *Aa* = "alba"; *aa* = yellow ♀.

sentially the same autosomal genotype and that the "alba" gene in females causes the spot to be paler than in homozygous recessive *aa* females. The histogram is for the largest brood available (F_1 of ♀ 1920); the same trend is found in the other broods (see Table). This spot-color relationship be-



Proportions of discal spot color types in GEROULD'S Brood 1920*c*. Each block shows the percentage of ♂♂ or "alba" ♀♀ or *aa* ♀♀ showing the indicated color (*e.g.*, 0.6 of all ♂♂ had the spot yellow).

tween males and yellow females is the opposite of that for ground-color, in which the female has distinctly paler yellowness than does the male. The following equivalents seem to be justified:

Genotype I: ♂ pale yellow = "alba" ♀ yellow = *aa* ♀ yellow
Genotype II: ♂ yellow = "alba" ♀ pale semi-orange = *aa* ♀ semi-orange
Genotype III: ♂ pale semi-orange = "alba" ♀ semi-orange = *aa* ♀ deep semi-orange
Genotype IV: ♂ semi-orange = "alba" ♀ deep semi-orange = *aa* ♀ orange
Genotype V: ♂ orange = "alba" ♀ orange = *aa* ♀ red-orange.

Genotypes I and V seem to be rare among several hundred wild yellow (*aa*) females examined from eastern and western U.S.A. and Canada.

The genetic control of the different spot types is not entirely clear. The principal difficulty comes from the complete lack in my data of these important crosses: Type I × Type I; Type V × Type V; and Type I × Type V. The data available suggest that there are one or two pairs of genes principally controlling the color of the hindwing discal spot. As with the general ground-color of the wings, it is likely that environmental effects and modifier gene complexes influence the phenotypic expression of the basic, or "switch," genes for yellowness or redness of the discal spot. These "basic" genes seem to be acting as blending factors, with alleles for both yellow and orange expressed phenotypically.

KOMAI and AÉ (1953) suggested that the color of the discal spot in males of *C. erate poliographus* Motsch. may be controlled by a single pair of genes, with orange dominant over pale yellow. Their data were very limited, and they did not report the color of the spot in females, so it is not possible to interpret their work on the basis of the present studies.

A painstaking study of "alba" females of both *C. philodice* and *C. eurytheme* was carried out in the hope of finding discal spot differences by which heterozygous (*Aa*) "alba" females could be distinguished from homozygous (*AA*) "alba" females. This attempt was unsuccessful. However, it may be possible to find differences if a large series of absolutely certain homozygous *AA* "alba" females is available for comparison with known heterozygotes, such as our brood #61, which includes 32 "alba" females all known to be *Aa.*

No attempt has yet been made to analyze the geographic correlation of the relative frequency of the discal spot types. HOVANITZ (1945) found the spot darker in Alaskan than in more southern populations of *C. philodice.*

It has been suggested by some that the color of the discal spot is a species-recognition character for *C. philodice* and its close relative, *C. eurytheme.* The latter has the spot red-orange in males and in *aa* (orange) females. The widespread occurrence of orange spots in *C. philodice* might be considered to have been due to introgression of the orange gene into *C. philodice* following recent hybridization with *C. eurytheme.* This possibility seems to be ruled out by the fact that individuals with orange discal spots are even more numerous than those with yellow spots among the series of New England *C. philodice* collected prior to the arrival of *C. eurytheme* in New England and now preserved at Yale and in the Museum of Comparative Zoology at Harvard.

This paper has been extensively revised since it was cited in my review (Remington, 1954). When the first version was written, the Gerould Collection was not available, and certain Connecticut broods had not yet been mounted for study. It had appeared at first that the allele for yellow is recessive to the allele for orange.

SUMMARY

In *Colias philodice* from New England the yellow or orange color of the discal spot on the upper side of the hindwings appears to be controlled by one or two pairs of autosomal genes expressed as blending factors. With identical genotypes, males have phenotypically the lightest (yellowest) spot; it is deeper in "alba" females and deepest (reddest) in yellow females.

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