HEREDITY OF BODY COLOR IN DROSOPHILA

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FOUR COLORED FIGURES—PLATE 1

Cultures of the fruit fly, Drosophila ampelophila, have given rise to three mutations in the color of the body and wings. The origin of these new types has been briefly described in a preliminary note, and some of the main facts connected with their inheritance have been given there, but the principal data on which the statements rest have been reserved until the present time. The results include 81,070 counts. It may be asked what advantage is there in doing the experiments on so large a scale. Why would not a few cases with suitable tests show the mode of inheritance of the factors involved? The answer is two-fold. The question of the relative viability can only be determined in this way, and for further work with these body colors it is necessary to know what rôle this condition plays in the numerical results. In the second place it seemed worth while to illustrate on a large scale the phenomenon of sex-linked inheritance. It is an impressive fact, for instance, to find in the F_2 generation (out of black female by brown male) 6124 black females, 3015 black males and 2472 brown males. Not a single brown female in 11,000 grandchildren. While in the reciprocal cross there are present 2191 black females, 1987 black males, 1532 brown females and 1448 brown males. Such results cannot fail, I think, to impress those who take a sceptical attitude toward the modern study of heredity.

The black and the yellow mutants arose directly and independently from inbred, normally colored, or gray flies. The brown flies were produced by crossing and extracting. They also arose independently in cultures related to the black flies but were at first supposed to be a particular kind of yellow fly which was recognized, however, as different from the ordinary yellow and had been maintained in a separate culture. When, however, in the second generation from black and yellow these same flies appeared, their relation to the other colors was apparent. Forms like these, that represent a type due to absences, derivable through combination of primary mutations may be said to arise by permutation.

In making the counts I have been assisted by Miss E. M. Wallace, Miss Eleth Cattell and Mr. C. B. Bridges. In practically all cases I have checked up each count after the separation had been made, so that the results stand for the agreement of two observers. Only in the case of separation of yellows and browns could any disagreement arise, and while I cannot claim for this case that the separation has been exact, I think that it is very nearly so.

Description of the mutants

The color differences between the normal, wild, or gray fly and the mutants is shown by the accompanying plate, figures 1 to 4. The detailed comparisons are as follows:

The wild fly. The upper surface of the thorax is olive yellow, the olive shade being very faint. As the flies get older the color deepens. Some of the wild flies have a black trident and two lateral black streaks on the upper surface of the thorax (not shown in the present case), but many flies do not show this marking. I have made a long series of selection experiments with this marking and have produced one race that never shows the trident, and another race that has a dark well-developed trident. How far the character is a fluctuating one and how far due to genotypic difference need not be discussed here.

The abdomen of the female is banded with lemon yellow and black. In the male there are only two black bands as a rule; the end of the abdomen is black. The legs are colored like the thorax but somewhat lighter. The hairs on the body are black.

The wings are very transparent, blue gray or smoky. The veins appear dark, but under the microscope are seen to be brownish yellow. There are no dark bands along the sides of the veins. The upper surface of the head of the wild fly, and also of the mutants is colored like the thorax. The under surface of the abdomen is more yellow in the male, than in the female.

The yellow fly. The upper surface of the thorax is yellow ochre in color and lighter than that of the wild fly. It is interesting to observe that the dark marking or shield is always absent from the yellow flies.

The light bands on the abdomen are of the same color as the thorax, i. e., pure yellow ochre, and lighter than those of the wild fly. The dark bands are brown. The legs are the same color as the thorax. The veins of the wings are yellow like the thorax. The interspaces (or background) are of a transparent golden yellow and strongly contrast with the color of the wings of the wild fly. The hairs are brown, instead of black as in the wild fly.

The black fly. The upper surface of the thorax is the same general color as that of the wild fly, but darker in the sense of being browner. The black trident is always present and conspicuous, and the two lateral markings are also conspicuous. The trident is not only well developed, but appears to be longer and narrower than that of the normal. It is one of the most striking features of the black mutant. The light bands of the abdomen are darker than those of the normal, but not so dark as is the thorax. The dark bands are very black. The legs are blacker than the legs of the wild fly, especially the more distal parts. The hairs on the body are black. The veins of the wings are very black. On each side of each vein there is a dark (semitransparent) band. The interspaces between these bands are gray, but darker than the gray of the wing of the wild fly. While the black fly is blacker than the wild fly in nearly all of its parts, so that a heap of them is very dark compared with a heap of the normal flies, the most striking character that distinguishes them from the other types is the dark wings with the dark bands on the sides of the veins.

The brown fly. The upper surface of the thorax is brown. The brown color deepens as the fly gets older, and the color shown in the figure is that of an older fly. When first hatched the brown is more yellowish in shade, and not so easily distinguished from that of the older yellow flies. Most of the brown flies, especially the older ones, show a brown shield on the thorax, in form like that on the thorax of the black fly. The light bands of the abdomen are light brown and differ therefore from the yellow bands of the yellow fly. The dark bands are brown. The legs also show some brown. The veins of the wings are brown like the thorax. On each side of each vein is a brown band. It is by means of these bands that one can most readily separate under a lens the yellow from the brown fly. The interspaces between the bands are gray-brown, and more transparent than the bands. The hairs are also brown.

In separating the flies into the color groups, (after slightly etherizing) there is never any difficulty in distinguishing the gray from the black and from the yellow, provided they have not just hatched; but the yellow flies and the brown offer greater difficulties, especially when flies of different age are mixed together, and when small flies are also present, due to starving the larvae. I do not feel certain that the separation of these two groups has been always perfect, but the errors are not great enough I think to vitiate seriously the classification. In some cases I have kept the flies alive for several days in order to verify my first separation, and have found occasionally that one or two flies have been put into the wrong group. The errors have been in both directions, and counterbalance to some extent. I have followed the rule of classifiying flies as brown only when they were certainly brown, as shown best by the broad brown bands along the veins of the wings, and this has lead, I fear, to the inclusion of a few brown flies in the yellow group. I have also tested my ability to separate these two groups by breeding doubtful flies, which, in general, I would have placed in the yellow category. If the fly in question is a yellow female and is bred to a black male, all the female offspring should be gray (because only the female producing sperm carries the factor for black) and all the males should be yellow. If the fly in question were a brown female, and were bred to a black male, all the female offspring should be black and all the males brown. In general I have found my separation to be correct. The difficulty has arisen apparently in most cases with heterozygous yellow females that contain only one dose of yellow instead of two, as does the ordinary pure yellow. In such cases two classes of females appear when crossed to black males, namely, gray and black,

In regard to the distribution in the wild fly of the products of the three color factors, that go to produce its color, it is difficult to speak with certainty, but from comparison with corresponding regions in the mutants when one or another of the color factors is absent it appears that the black regions are due to the black factor, but the brown may be present and overlaid by the black. At least it may be said that the black regions in the gray fly and in the black fly are brown in the brown fly, but of course it is possible that when the black develops the brown may not develop, or the black may even be a further stage of development of the brown pigment. The yellow of the wild fly also seems to replace the brown of the brown fly at least when yellow is absent the color of the yellow regions is brown. Possibly, as I have suggested, yellow when present inhibits brown, for otherwise it is difficult to see how the yellow fly should be lighter in color than the brown fly.

The black flies are large and vigorous. There is no difficulty in breeding them or in crossing. The yellows are generally smaller (though not always) and are more delicate. They get stuck very easily to the moist sides of the culture bottles, and, being unable to free themselves, perish. They are more difficult to breed and to cross. The brown flies although generally large are weak. They get stuck to the food and to the walls of the bottles and die. Otherwise they seem healthy. On the whole the mutants are weaker than the normal flies, but the loss of the yellow factor that produces the black flies is less injurious then the loss of the black factor that produces the yellow fly. I have at times thought that the loss of both of the factors produces the weakest fly in the series—the brown fly— but this is difficult to prove.

Formulas

The color of the wild fly appears to be due to the presence of three factors, Black (B), Yellow (Y) and Brown(Br). For brevity this color is spoken of as Gray, which corresponds nearly to the color of the semi-transparent wings. If the black factor (B) is absent (b) the color of the fly is yellow (Y), more especially the wings. The yellow fly is therefore bYBr. Where the factor for yellow (Y) is absent (y) the fly is black, more especially the wings. The black fly is therefore ByBr. When both black and yellow are absent the fly is brown, more especially the wings. The brown fly is, therefore, byBr. The brown fly can always be produced by crossing yellow and black and inbreeding the F_1's which give by recombination some Browns in the second, F_2, generation. Of course, the same result would follow if both yellow and black were lost from the gray fly at the same time, but this is unlikely since the black and the yellow factors lie in different parts of the hereditary complex.

Of these three color factors that of black is sex-linked; the yellow factor is not sex-linked, and is contained in all gametes both in the male and in the female of gray and yellow flies. One must be careful to observe that while the *factor* for black is sex-linked the black fly, bred to gray does not show sex-linked (sex-limited) inheritance; while the yellow fly bred to normal shows sex-linked inheritance. This will be clear from an examination of the analyses given below.

All possible crosses have been made between these mutants, and, these may now be taken up in order.

Wild (gray) by black

When the female wild flies (Gray) are mated to male black flies all of the offspring are gray. These F_1 gray flies are darker than the wild flies, i. e., they are to some extent intermediate in color between gray and black. It is true that there is much variation in these hybrids, and some flies can not always with certainty be distinguished from wild flies, but most of them are undoubtedly distinctly darker, especially the wings. How this could occur may not appear clear at first sight, for both the wild gray females and the gray-black hybrids contain two doses of black—the only difference between the two is the absence of one dose of yellow, in the hybrids. If, in the absence of this dose of yellow, the black has a better chance to show itself more positively, we can account for the intermediate character of the hybrid. If such is the case, the yellow factor is to some extent a partial inhibitor of black. The same explanation applied to the males is as follows: the wild gray male has only one dose of black (since black is sex-linked). It has two doses of yellow. The hybrid has also one dose of black (B) but only one dose of yellow. It differs, therefore, from the wild male in having one dose of yellow instead of two. The darker color of the hybrid male would, in consequence, be due to relatively less yellow than that present in the wild male. The explanation is the same therefore for both sexes, but it involves the assumption that the color of the wild female which is the same as that of the male is due to the presence of a double dose of B and Y(BY, BY) while the color of the wild male is due to one dose of black and two of yellow (BY, Y). Removal of one Y from the wild female makes her darker; and similarly the removal of one Y from the wild male makes him darker also.

The numerical results for the F_2 generation are as follows:

G ♀ by B ♂ =	G ♀, G ♂ =	Gray ♀	5053
		Gray ♂	4861
		Black ♀	1280
		Black ♂	1385

The expectation, as shown by the analysis below, calls for three grays to one black. There are 9914 grays and 2665 blacks. The blacks fall considerably below expectation, yet the black flies are a vigorous strain and appear in the cultures to breed as well as the grays.

It will be noted that while the gray males run some 200 flies behind the females, the black males exceed the females by 100 flies.

Since these counts are from more complex crosses involving white eyes and short wings as well as red eyes and long wings, and since the former characters are associated at times with diminishing returns, I give in the next table some results where only black and gray color are involved:

G ♀ by B ♂ =	G ♀, G ♂ =	Gray ♀	867
		Gray ♂	811
		Black ♀	201
		Black ♂	180

There are 1678 grays and 381 blacks. The ratio is approximately four to one which is not very different from the preceding ratio. The analysis of this cross is as follows:

	Gray ♀ BYBrX — BYBrX Black ♂ ByBrX — byBr
F_1	Gray ♀ BYBrX — ByBrX Gray ♂ BYBrX — byBr
Gametes of F_1	BYBrX — ByBr BYBrX — ByBrX — byBr — bYBr
F_2	Gray ♀ 3 Black ♀ 1 Gray ♂ 3 Black ♂ 1

The reciprocal cross, gray male by black female gave the following results:

B ♀ by G ♂ =	Gray ♀, Gray ♂ =	Gray ♀	1465
		Gray ♂	1453
		Black ♀	344
		Black ♂	299

The expectation is here also three grays to one black. The total for the grays is 2918, and for the blacks 643, which is about $4\frac{1}{2}$ to 1. In the grays, the males and females are nearly equal, while in the blacks, the females exceed the males by a fair margin. Since these numbers also are derived from mixed counts (as before) I give below a count involving only the two colors in question:

B ♀ by G ♂ =	Gray ♀, Gray ♂ =	Gray ♀	836
		Gray ♂	875
		Black ♀	209
		Black ♂	148

There are 1711 grays and 357 blacks which is very nearly 5 to 1.

Wild (gray) by yellow

The results of this cross have been already published (1911), but may be given here for the sake of completeness. In both cases the parents were alike except for body color:

G ♀ by Y ♂ =	Gray ♀ 654 Gray ♂ 705	=	Gray ♀ Gray ♂ Yellow ♂	525 340 194

The sum of the males is here nearly equal to the females as called for in the expectation (see below). It will be noted, however, that the gray males in F_2 greatly exceed the yellow males, and that the gray males are considerably more than half (268) the gray females.

It may seem that the discrepancy in the yellow males is not due to their viability alone, but rather that the gray-bearing male-producing spermatozoa are more likely to fertilize the eggs than are the yellow bearing sperm. The analysis is as follows:

	Gray ♀ BYBrX — BYBrX Yellow ♂ bYBrX — bYBr
F_1	Gray ♀ BYBrX —bYBrX Gray ♂ BYBrX — bYBr
F_2	Gray ♀ 2 Gray ♂ 1 Yellow ♂ 1

The reciprocal cross is as follows:

Y ♀ by G ♂ =	G ♀ 397 G ♂ 282	=	Gray ♀ Gray ♂ Yellow ♀ Yellow ♂	346 259 226 230

The excess of females in F_1 is noticeable. The expectation in F_2 is equal numbers for all classes. The grays run ahead of the yellows. There is a very noticeable deficiency in the gray males compared with the gray females. The analysis is as follows:

	Yellow ♀ bYBrX — bYBr ♀ Gray ♂ BYBrX — bYBr ♂	
F_1	Gray ♀ bYBrX — BYBrX ♀ Gray ♂ bYBrX — bYBr ♂	
F_2	Yellow ♀ 1 Yellow ♂ 1 Gray ♀ 1 Gray ♂ 1	

Black by yellow

Black females mated to yellow males give gray females and males. The data for F_2 are:

B ♀ by Y ♂ = {G ♀, G ♂} =

Gray	♀	5147
Gray	♂	2451
Black	♀	1591
Black	♂	750
Yellow	♂	1957
Brown	♂	530

The expectation is for the females, gray 6, black 2; and for the males, gray 3, black 1, yellow 3, brown 1. There are nearly 374 more gray females than 3 times the black females. There are also 500 more gray males than yellow males. Both excessive classes correspond to the F_1 classes. There are more black females than two times the black males. The analysis is as follows:

	Black ♀ ByBrX — ByBrX ♀ Yellow ♂ bYBrX — bYBr ♂
F_1	Gray ♀ ByBrX — bYBrX ♀ Gray ♂ ByBrX — bYBr ♂
Gametes of F_1	BYBrX — ByBrX — bYBrX — byBrX ♀ BYBrX — ByBrX — bYBr — byBr ♂
	Gray ♀ 6 Gray ♂ 3 Black ♀ 2 Black ♂ 1 Yellow ♂ 3 Brown ♂ 1

The reciprocal cross yellow females by black males gives gray females and yellow males. The numerical data follow:

Y ♀ by B ♂ =	G ♀, Y ♂ =	Gray ♀	2442
		Gray ♂	1893
		Black ♀	1893
		Black ♂	723
		Yellow ♀	1547
		Yellow ♂	1548
		Brown ♀	441
		Brown ♂	428

The expectation for the females and males alike is gray 3, yellow 3, black 1, brown 1. There are about 900 more gray females than yellow females; while the gray males are only 350 more numerous than the yellow males. The gray females and yellow males are the F_1 classes. The yellow females are as numerous as the yellow males. The black males are about a third of the gray males and more than this ratio in regard to the yellow males. The blacks run well ahead of the browns, the females being more than four times as numerous. The analysis is as follows:

	Yellow ♀	bYBrX — byBrX
	Black ♂	ByBrX — byBr
F_1	Gray ♀	byBrX — ByBrX
	Yellow ♂	bYBrX — byBr
Gametes of F_1		byBrX — bYBrX — ByBrX — BYBrX ♀
		byBrX — bYBrX — byBr — bYBr ♂

F_2	Brown ♀ 1	Brown ♂ 1
	Yellow ♀ 3	Yellow ♂ 3
	Black ♀ 1	Black ♂ 1
	Gray ♀ 3	Gray ♂ 3

Wild (gray) by brown

When the normal (Gray) females were mated with brown males all the offspring were gray. The numerical results for F_1 and F_2 were as follows:

G ♀ by Br ♂ =	G ♀ 266 =	Gray ♀	2618
	G ♂ 236	Gray ♂	1342
		Black ♀	765
		Black ♂	351
		Yellow ♂	985
		Brown ♂	300

The expectation is six gray females to two black females, and for the males 3 gray, 3 yellow, one black, one brown. The normal females are almost exactly twice the number of normal males. The normal males exceed three times the black males by nearly 300; and the black males exceed the brown males 50 flies. The yellow males are somewhat more than three times as numerous as the brown males, but less than three times as numerous as the black males. The yellow males, which should be as numerous as the normal males are about 350 fewer. The sum total of all the females is 3383 and of the males 2988. The males are about 400 flies fewer than the females.

Despite these differences the numbers accord fairly well with the expectation, at least the classes stand in the same general relation that the analysis calls for. The analysis follows:

	Gray ♀ YBBrX — YBBrX Brown ♂ ybBrX — ybBr	
F_1	Gray ♀ YBBrX — ybBrX Gray ♂ YBBrX — ybBrX	
Gametes of F_1	yBBrX — YBBrX — ybBrX — YbBrX ♀ yBBrX — YBBrX — ybBr — YbBr ♂	
F_2	Black ♀ 2 Gray ♀ 6	Black ♂ 1 Gray ♂ 3 Yellow ♂ 3 Brown ♂ 1

The reciprocal cross, brown females by gray males gave gray females and yellow males. The numerical data for the F_1 and

F_2 generation are as follows. The counts of the F_1 flies are taken from another similar cross.

Br ♀ by G ♂ =	G ♀ 124 / Y ♂ 111 =	Gray ♀	406
		Gray ♂	171
		Black ♀	74
		Black ♂	55
		Yellow ♀	162
		Yellow ♂	190
		Brown ♀	37
		Brown ♂	51

Owing to the failure of many of the brown females to breed the numerical results are small. The expectation for the females is gray 3, black 1, yellow 3, brown 1, and for the males, gray 3, black 1, yellow 3, brown 1. It will be observed that the gray females greatly exceed the yellow females while the yellow males exceed slightly the gray males. The F_1 females are gray and the males yellow.[1] The analysis follows:

	Brown ♀	ybBrX — ybBrX
	Gray ♂	YBBrX — YbBr
F_1	Gray ♀	ybBrX — YBBrX
	Yellow ♂	ybBrX — YbBr
Gametes of F_1	YbBrX — ybBrX — YBBrX — yBBrX ♀	
	YbBrX — ybBrX — YbBr — ybBr ♂	

Gray ♀	3	Gray ♂	3
Black ♀	1	Black ♂	1
Yellow ♀	3	Yellow ♂	3
Brown ♀	1	Brown ♂	1

Black by brown

When black females are mated to brown males all the offspring are black. The numerical data for F_1 and F_2 are as follows:

B ♀ by Br ♂ =	B ♀ 299 / B ♂ 274 =	Black ♀	6124
		Black ♂	3015
		Brown ♂	2472

[1] In another experiment the gray males equalled the gray females.

The expectation is that the black females shall be as numerous as the sum of the two classes of males; there are about 600 too few males owing largely to a deficit in the brown class which runs about 450 behind the black males. The analysis follows:

	Black ♀ yBBrX — yBBrX Brown ♂ ybBrX — ybBr
F_1 and gametes of F_1	Black ♂ yBBrX — ybBrX Black ♀ yBBrX — ybBr
F_2	Black ♀ 2 Black ♂ 1 Brown ♂ 1

The reciprocal cross, brown females and black males gives black females and brown males. The numerical data are as follows:

Br ♀ by B ♂ = {B ♀, Br ♂} =

Black ♀	2191
Black ♂	1987
Brown ♀	1532
Brown ♂	1448

The expectation is equality throughout; but the Browns run, class for class, about 600 behind the Blacks. The analysis gives:

	Brown ♀ ybBrX — ybBrX ♀ Black ♂ yBBrX — ybBr ♂
F_1	Black ♀ ybBrX — yBBrX ♀ Brown ♂ ybBrX — ybBr ♂
F_2	Brown ♀ 1 Brown ♂ 1 Black ♀ 1 Black ♂ 1

Yellow by brown

Yellow females by brown males give yellow females and males. The numerical data are:

Y ♀ by Br ♂ = {Y ♀ 115, Y ♂ 99} = {Yellow ♀ .... 2295; Yellow ♂ .... 2232; Brown ♀ .... 830; Brown ♂ .... 758}

The expectation is three yellows to one brown, and the numbers approximate to this relation. When the difficulties of separating these two classes is taken into account the agreement is remarkably close. The analysis follows:

Yellow ♀ YbBrX — YbBrX
Brown ♂ ybBrX — ybBr

F_1	Yellow ♀ YbBrX — ybBrX ♀ Yellow ♂ YbBrX — ybBrX — ybBr — YbBr
F_2	Yellow ♀ 3 Yellow ♂ 3 Brown ♀ 1 Brown ♂ 1

The reciprocal cross, brown females by yellow males, gives yellow females and males. The numerical data are:

Br ♀ by Y ♂ = {Y ♀ 129, Y ♂ 102} = {Yellow ♀ .... 1181; Yellow ♂ .... 1409; Brown ♀ .... 571; Brown ♂ .... 520}

The expectation is again three yellows to one brown; and this is fairly well realized. There are more yellow males than yellow females, and slightly more brown females than brown males. The analysis is as follows:

Brown ♀ ybBrX — ybBrX
Yellow ♂ YbBrX — YbBr

F_1	Yellow ♀ ybBrX — YbBrX Yellow ♂ ybBrX — YbBrX — YbBr — ybBr
F_2	Yellow ♀ 3 Yellow ♂ 3 Brown ♀ 1 Brown ♂ 1

DISCUSSION

The color of the body of the wild fly appears from the experimental data to be due to at least three factors viz., yellow, black, brown. It has been shown in a former paper that the red eye of the wild fly is also due to the presence of three factors viz., vermilion, pink, orange. In both series one at least of the three factors is sex-linked; the factor for black in the one and for pink in the other. In crossing both series give almost parallel results. In the eye-color series the factor for orange is always present, either simplex or duplex. In my former paper I could not determine whether it is sex-linked or not, because it had never dropped out, but since then I have obtained a new mutation in which orange has dropped out, and, by suitable experiments, it has been shown that this factor also is sex-linked. It appears then that in the eye color series there are two sex-linked factors, P and O, and one not sex-linked, V. In the present series brown occupies a similar position in the symbolism used to that of the orange factor in the eye color series, but on the basis of this similarity it would not be justifiable to conclude that the brown factor is sex-linked.

In this connection I may record that during the summer of 1910 there appeared for a time, in one of my cultures, flies that had almost no color in the body although the eyes were red. A few pigment granules brownish in color were scattered over the abdomen. The flies resembled in some respects flies that had just emerged from the pupa case. The flies were extremely weak and died after a few days without progeny. Whether they represent the loss of the brown factor, or of the color producer can not be stated. Since they appeared in cultures of gray flies the latter interpretation seems more probable.

Whether the comparison drawn above between the eye color series and the body color series has any real significance can, of course, be only a matter of conjecture. It should be pointed out that any eye color may be combined with any body color, and I have been unable to detect any correlated effect of these two combinations upon each other, except such effect as is due to color contrast.

One can not work with these body colors without being impressed by the similarities between the brown and the black flies on the one hand, and the yellow and the gray on the other. Brown and black lack the yellow factor, and if this, as I suppose, acts to some extent as an inhibitor the resemblance is manifest; while conversely the presence of the yellow factor in the yellow and in the normal fly makes clear their resemblance. One is tempted to surmise that black and brown may both be stages of the same chemical reaction, which surmise would be more probable if it could be shown that both factors are contained in the X chromosome, but this relation in itself could not be used as an argument to urge their dependent chemical nature.

PLATE 1

EXPLANATION OF FIGURES

1 Normal or gray female (the outer marginal vein is slightly exaggerated in the figure).

2 A black female.

3 A brown female.

4 A yellow female. The contrast between the black, yellow, and brown flies is well brought out in the figures.

PLATE 1

1

2

3

PHOTO-CHROMOTYPE, PHILA-PA

4

E. M. WALLACE, DEL.