DATA FOR THE STUDY OF SEX-LINKED INHERITANCE IN DROSOPHILA

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In recent years a new fact in Mendelian inheritance has come to light, which while it obscures the Mendelian expectation based on *independent* segregation of the factors of inheritance, shows that the main Mendelian principles are by no means invalidated; for, they too are manifest, but obscured by the linkage or coupling of certain factors. When certain somatic characters are associated with sex, as in Drosophila, we have the best opportunity, as yet afforded, for studying in its simplest form this sort of 'associative' inheritance; for, in certain combinations, the relation between linkage and breaking of the linkage ('crossing-over' as we shall call it) is shown at once by the male flies which indicate without complication the kinds of eggs that the F_1 female produces. In certain combinations both males and females give this result. Such cases are those in which the sperm of the F_1 generation contains only sex-linked recessive or 'absent' characters.

In the following account we shall describe certain experiments in which three linked characters (in addition to sex) are involved; namely, red eyes, versus no red or white eyes; the black factor for body color (giving black or gray flies), versus its absence (which gives yellow or brown flies); and the factor for long wings versus the absence of that factor (which gives miniature wings). These characters show various strengths of linkage, i.e., the number of times any two of them hold together differs for each combination. This relation will be discussed after the data have been given.

Since these sex-linked factors follow the distribution of the sex-chromosomes we may think of them as contained in these chromo-

somes (X) when present, or absent from the chromosomes when the absence of the factor is involved. In the male-producing sperm, where no X is present, the sex-linked characters are always absent. A corollary to this point of view involves the crucial point of the chromosome theory of linkage (Morgan, '11). In the female two X-chromosomes are always present. If one of them contains two of the factors in question, such as the factor for red[1] (R) and that for long wings (L), and the other X-chromosome contains no factor for red (absence of red or W) and short wings (or S) it is possible for interchange (or 'breaking,' or 'crossing-over') between RL and WS to take place. How often this may occur depends on the strength of the linkage of the factors involved (which one of us has tried to interpret as due to their position in the chromosomes). But in the male, on the other hand, no such interchange is theoretically possible, and the results show that none occurs. It is this simple and consistent relation that gives 'point' to the chromosomal interpretation.

In order to have a basis for interpreting the more complicated cases we will first give the results of an experiment where only two contrasted characters, black and yellow, are involved. In this experiment no question of linkage is involved, since the factor for black and that for yellow are not in the same chromosome. The experiment also gives information showing the viability of the gray, black, yellow and brown flies.

When black females were mated to yellow males all the offspring were gray (N). These inbred gave the following results:

	LRB ♀ by LRY ♂
F_1	LRN ♀ = 50 LRN ♂ = 60
F_2	LRN ♀ = 316 LRN ♂ = 153 LRB ♀ = 104 LRB ♂ = 48 LRY ♂ = 164 LRBr ♂ = 40

[1] In reality the presence of C gives red and its absence c white

The analysis is as follows:

	yBBrX – yBBrX	Black ♀
	YbBrX – YbBr	Yellow ♂
F_1	yBBrXYbBrX	Gray ♀
	yBBrXYbBr	Gray ♂

Gametes F_1: YBBrX – yBBrX – YbBrX – ybBrX (Eggs); YBBrX – yBBrX – YbBr – ybBr (Sperm)

F_2	YBBrXYBBrX	Gray ♀	YBBrXYbBr	Gray ♂
	YBBrXyBBrX	Gray ♀	YBBrXybBr	Gray ♂
	yBBrXYBBrX	Gray ♀	yBBrXYbBr	Gray ♂
	yBBrXyBBrX	Black ♀	yBBrXybBr	Black ♂
	YbBrXYBBrX	Gray ♀	YbBrXYbBr	Yellow ♂
	YbBrXyBBrX	Gray ♀	YbBrXybBr	Yellow ♂
	ybBrXYBBrX	Gray ♀	ybBrXYbBr	Yellow ♂
	ybBrXyBBrX	Black ♀	ybBrXybBr	Brown ♂

Summary of F_2	Gray ♀ 6	Gray ♂ 3
	Black ♀ 2	Yellow ♂ 3
		Black ♂ 1
		Brown ♂ 1

The numbers fairly approximate to expectation. The reciprocal cross is as follows:

LRB ♂ by LRY ♀

F_1	LRN ♀ = 89
	LRY ♂ = 59
F_2	LRN ♀ = 212
	LRN ♂ = 197
	LRB ♀ = 79
	LRB ♂ = 69
	LRY ♀ = 181
	LRY ♂ = 188
	LRBr ♀ = 44
	LRBr ♂ = 71

The analysis follows:

	YbBrX – YbBrX	Yellow ♀
	yBBrX – ybBr	Black ♂
F_1	YbBrXyBBrX	Gray ♀
	YbBrXybBr	Yellow ♂

Gametes F_1	ybBrX	– YbBrX	– yBBrX	– YBBrX	Eggs
	ybBrX	– YbBrX	– ybBrX	– YbBr	Sperm

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

The results agree again fairly well with the expectation. The numbers of gray males and females are quite close. This correspondence between the sexes holds throughout, although the females exceed the males in the grays and blacks, while the males are in excess in the yellows and browns.

In the next case also the same two characters are involved, viz., yellow and black, but combined with short (miniature) wings and white eyes. The analysis is the same as in the last case, and need not be repeated:

SWB ♀ by SWY ♂

F_1	SWN	♀	= 78
	SWN	♂	= 62
F_2	SWN	♀	= 355
	SWN	♂	= 173
	SWB	♀	= 111
	SWB	♂	= 44
	SWY	♂	= 149
	SWBr	♂	= 42

The reciprocal cross was also made:

SWY ♀ by SWB ♂

F_1	SWY	♂	= 88
	SWN	♀	= 69
F_2	SWN	♀	= 68
	SWN	♂	= 71
	SWB	♀	= 10
	SWB	♂	= 11
	SWY	♀	= 38
	SWY	♂	= 64
	SWBr	♀	= 12
	SWBr	♂	= 11

CROSSES INVOLVING TWO SEX-LINKED CHARACTERS

In the following crosses black and yellow body-color, white and red eyes are involved. In these cases there are only two sex-linked factors, viz., the factor for black and the factor for red (and their respective absences). In reality, it is the color-producer, C, and not red color, R, that is the factor involved in the eye-color inheritance; but with this explanation no misunderstanding will arise if we use the symbol R for red eye and W for its absence.

In the first case long winged, white eyed, black females were crossed with long winged, red eyed, yellow males. If all the female classes were realized in F_2 there would be many more classes than actually appear, but owing to the linkage between W and B from the grandmother, and R and b from the grandfather there will be only eight large classes. The smaller classes represent the breaking of the linkage or 'crossing-over:'

LRY ♂ by LWB ♀

F_1	LRN ♀	= 244
	LWN ♂	= 253
F_2	LRN ♀	= 1549
	LRB ♀	= 490
	LWN ♀	= 1120
	LWN ♂	= 1283
	LWB ♀	= 368
	LWB ♂	= 451
	LRY ♂	= 1042
	LRBr ♂	= 217
	LRN ♂	= 3
	LWY ♂	= 1
	LRB ♂	= 1

The analysis is as follows. The factor for Brown (Br) is here omitted:

	WByX – WByX	White black ♀
	RbYX – WbY	Red yellow ♂
F_1	WByXRbYX	Red gray ♀
	WByXWbY	White gray ♂
Gametes of F_1	WBYX – WByX – RbYX – RbyX	Eggs
	WBYX – WByX – WbY – Wby	Sperm
F_2	Gray white ♀ 3	Gray white ♂ 3
	Gray red ♀ 3	Yellow red ♂ 3
	Black white ♀ 1	Black white ♂ 1
	Black red ♀ 1	Brown red ♂ 1

There were five cases of crossing-over of color factors in the males, in a total of 2993 males; approximately, once in 600 times. The crossing-over was between Rb and WB. Each time that the crossing-over occurs one way, there should be on an average a counter-cross the other way. Thus, when an interchange between Rb and WB takes place the combination RB will occur as often as Wb. We should expect, therefore, to find a balance in the results, except in so far as accident or death obscure the output. In the present case the cross-over RB survived four times (giving 3, LRN and 1, LRB), while the counter-cross Wb survived only once. Three of the counter-crosses are not represented. The result can probably be explained by the lower viability that exists for the Yellow-whites.

The reciprocal cross is given below. There were also eight large classes but no cases of crossing-over. The numbers are much fewer than in the last case.

LRY ♀ by LWB ♂

F_1	LRN ♀ = 255
	LRY ♂ = 262
F_2	LRN ♀ = 111
	LRB ♀ = 27
	LWN ♂ = 92
	LWB ♂ = 15
	LRY ♀ = 71
	LRY ♂ = 127
	LRBr ♀ = 10
	LRBr ♂ = 26

The analysis is as follows:

	RbYX – RbYX	Red yellow ♀
	WByX – Wby	White black ♂
F_1	RbYXWByX	Red gray ♀
	RbYXWby	Red yellow ♂
Gametes of F_1	RbyX – RbYX – WByX – WBYX	
	RbyX – RbYX – WbY – Wby	
F_2	Brown red ♀ 1	Brown red ♂ 1
	Yellow red ♀ 3	Yellow red ♂ 3
	Black red ♀ 1	Gray white ♂ 3
	Gray red ♀ 3	Black white ♂ 1

The result conforms fairly with expectation; the Yellow red running behind.

In the next crosses a third combination was present. Six large classes are expected.

	LRB ♀ by LWY ♂
F_1	LRN ♀ = 57
	LRN ♂ = 48
F_2	LRN ♀ = 298
	LRN ♂ = 158
	LRB ♀ = 75
	LRB ♂ = 54
	LWY ♂ = 88
	LWBr ♂ = 37
	LWN ♂ = 5

The analysis follows:

	RByX – RByX	Red black ♀
	WYbX – WYb	White yellow ♂
F_1	RByXWYbX	Red gray ♀
	RByXWYb	Red gray ♂
Gametes of F_1	RBYX – RByX – WYbX – WybX	
	RBYX – RByX – WYb – Wyb	
F_2	Gray red ♀ 6	Gray red ♂ 3
	Black red ♀ 2	Black red ♂ 1
		Yellow white ♂ 3
		Brown white ♂ 1

There were five cases of crossing-over (males) in a total of 337 males. The cross-overs are all of one kind and result from the combination of W and B. The return crosses would be Red-yellows and these did not appear. The Red-yellows are, in fact, less viable than the White-blacks.

In the reciprocal cross eight large classes are expected. Only two classes of crossing-over were found. This again indicates a close union between R and B:

	LRB ♂ by LWY ♀
F_1	LRN ♀ = 198 LWY ♂ = 143
F_2	LRN ♀ = 341 LRN ♂ = 285 LRB ♀ = 153 LRB ♂ = 84 LWY ♀ = 253 LWY ♂ = 229 LWBr ♀ = 61 LWBr ♂ = 61 LWN ♂ = 6 LWB ♂ = 3

The analysis follows:

	WbYX – WbYX	White yellow ♀
	RByX – Wby	Red black ♂
F_1	WbYXRByX	Red gray ♀
	WbYXWby	White yellow ♂
Gametes of F_1	WbyX – WbYX – RByX – RBYX	
	WbyX – WbYX – Wby – WbY	
F_2	Brown white ♀ 1	Brown white ♂ 1
	Yellow white ♀ 3	Yellow white ♂ 3
	Black red ♀ 1	Black red ♂ 1
	Gray red ♀ 3	Gray red ♂ 3

There were nine cases of crossing-over, all males, in 659 males and 818 females. In this cross since all the F_1 sperm, both female and male-producing, carry only recessive sex-linked factors,

both sexes count in the ratio. This gives 9 to 1477 or 1 to 164. These cases are all in one direction. The missing counter-crosses should be Red-yellows.

The remaining cross involves the same combinations as one of the preceding, but the R and B factors are present in the gray fly. Therefore no crossing-over would be visible. Six large classes are expected:

LWB ♂ by LRN ♀

F_1	LRN (intermediate) ♀ and ♂ = 1085
F_2	LRN ♀ = 2714 LRN ♂ = 1541 LWN ♂ = 1033 LRB ♀ = 793 LRB ♂ = 330 LWB ♂ = 305

The analysis follows:

	RBYX – RBYX Red gray ♀ WByX – Wby White black ♂
F_1	RBYXWByX Red gray ♀ RBYXWby Red gray ♂
Gametes of F_1	RByX – RBYX – WByX – WBYX RByX – RBYX – Wby – WbY
F_2	Gray red ♀ = 6 Gray red ♂ 3 Black red ♀ = 2 Black red ♂ 1 Gray white ♂ 3 Black white ♂ 1

In the last case no evidence of crossing-over in the eye factors is expected; for, the normal and black flies are alike in that they carry the sex-linked factor for black. The yellow factor, it is true, is absent from Black and present in Normal, but it shows no linkage with White or with Red, which is in accord with the hypothesis here followed.

In the reciprocal cross eight large classes are expected, which occur. No crossing-over was expected or rather could have been observed even if it occurred:

LWB ♀ by LRN ♂

F_1	LWN (intermediate) ♀ 16 LRN (intermediate) ♂ 15
F_2	LRN ♀ = 1647 LRN ♂ = 1327 LRB ♀ = 449 LRB ♂ = 381 LWN ♀ = 1171 LWN ♂ = 1280 LWB ♀ = 379 LWB ♂ = 375

THE HEREDITY OF THREE CONTRASTED SEX-LINKED CHARACTERS

In the following crosses three contrasted sex-linked factors are involved, one for wings, one for eye color, and one for body color.

The factors involved are the same as those of the preceding crosses. Long wings (L) or normal wings contrast with miniature wings (S), recessive to the former. Two factors, both sex-linked, give, when both present, long wings, while miniature wings are due to the absence of one of them; the absence of the other producing the wing called rudimentary, but for simplicity the letters L and S may be used, if one remembers that L is in the X chromosome, and therefore present only in the female-producing sperm; while S merely means the absence of L, and alone stands for miniature wings.

The factor for red eyes (R) is also sex-linked (in the sense that the factor C is present); the absence of red is white eyes (W), which means that the factor C is absent; small c would express this condition more logically, but less graphically.

The black factor B is also sex-linked, and present, therefore, only in the female-producing sperm. Its absence is represented by small b. The factor for yellow (Y) is not sex-linked, and,

therefore, does not follow X in its distribution. Its absence is indicated by small y. In all there were five crosses with their reciprocals, or a total of ten combinations.

SRB ♀ by LWY ♂
SRB ♂ by LWY ♀
LWB ♀ by SRY ♂
LWB ♂ by SRY ♀
SWB ♀ by LRY ♂
SWB ♂ by LRY ♀
LRB ♀ by SWY ♂
LRB ♂ by SWY ♀
SRB ♀ by LWN ♂
SRB ♂ by LWN ♀

Three combinations, viz: the second, third and fourth gave some anomalous results and have been withdrawn in order that they may be repeated.

In representing the gametes of F_1 we have followed the plan of writing in the upper line of 'Eggs,' in the two middle terms, the two combinations that come direct from the paternal and maternal gametes, and at their sides, right and left, the eggs that come from the free distribution of Y and y. In the second line of eggs, written in similar sequence, are the crossing-over of long and short. The crossing of RB and Wb (or similar combinations) is not given, but can be readily conceived. It is the latter that gives the small classes of crossing-over for color (eye and body color) which follow the numerical data of the larger classes. The sperms are given in the third line of gametes and since by the hypothesis here followed no crossing-over in the gametes of the males is allowable, only one line (of four classes) is represented. In the sperm the yellow factor freely interchanges, since it shows no linkage with the sex-factor X. The results fully justify this assumption. Instead of writing out all the combinations of egg and sperm, a summary only of the expected results is given at the end of the analyses.

SHORT, RED, BLACK BY LONG, WHITE, YELLOW

When the female, SRB is mated to the male LWY all the female offspring are long, red, gray; and the males are short, red, gray. The results for the next F_2 generation are given below:

SRB ♀ by LWY ♂

F_1	LRN ♀ 98 SRN ♂ 80
F_2	LRN ♀ = 523 LRN ♂ = 146 LRB ♀ = 110 LRB ♂ = 31 SRN ♀ = 292 SRN ♂ = 242 SRB ♀ = 53 SRB ♂ = 82 LWY ♂ = 216 LWBr ♂ = 40 SWY ♂ = 85 SWBr ♂ = 30 LWN ♂ = 2 LRY ♂ = 1 SRY ♂ = 3 SWB ♂ = 1

The expectation is:

SRByBrX	– SRByBrX	Short red black ♀
LWYbBrX	– SWYbBr	Long white yellow ♂

F_1	SRByBrXLWbYBrX	Long, red, Gray ♀
	SRByBrXSWbYBr	Short, red, Gray ♂

Gametes of F_1	SRBYBrX –	SRByBrX –	LWbYBrX –	LWbyBrX	Eggs
	LRBYBrX –	LRByBrX –	SWbYBrX –	SWbyBrX	
	SRByBrX –	SRBYBrX –	SWbyBr –	SWbYBr	Sperm

L or SRN	♀ 6	S or LWY	♂ 3
L or SRB	♀ 2	S or LWBr	♂ 1
		L or SRN	♂ 3
		L or SRB	♂ 1

There were seven cases of crossing-over in color, all males, in a total of 872 males, or 1 to 97. Of these seven, three represent one crossing-over (LWN and SWB), and four the counter-cross. In this instance the balance is held despite the lesser viability of the Red-yellows.

The crossing-over of long, L, (normal) and short, S, (miniature) is shown in the large classes. The linkage is so 'loose,' that these two characters appear almost as though no linkage existed, but an examination shows that where S is combined with RB, and L with Wb the classes of SRB are relatively larger than those of LRB; while conversely the LWY classes are larger than the corresponding SWY. A comparison of the records with the expectation makes this evident at once. It is most apparent in the males, where no complications exist. Thus LWY ♂ = 216, while SWY ♂ = 85; LWB ♂ = 40, while SWB ♂ = 30, and on the other hand SRN ♂ = 242, while LRN ♂ = 146; and the SRB ♂ = 82, while LRB ♂ = 31. The sum of the 'straight' males is 580, while that of the cross-overs is 292. The gametic ratio is therefore 2:1.

SHORT, WHITE, BLACK BY LONG, RED, YELLOW

When the female is SWB and the male LRY the offspring are LRN ♀ and SWN ♂. The results in the next generation are given below:

SWB ♀ by LRY ♂

F_1	LRN	♀	228
	SWN	♂	181

F_2	LRN ♀	= 588
	LRB ♀	= 189
	LWN ♀	= 204
	LWN ♂	= 224
	LWB ♀	= 98
	LWB ♂	= 95
	SRN ♀	= 225
	SRB ♀	= 72
	SWN ♀	= 410
	SWN ♂	= 418
	SWB ♀	= 145
	SWB ♂	= 145
	SRY ♂	= 161
	SRBr ♂	= 47
	LRY ♂	= 419
	LRBr ♂	= 102
	LRB ♂	= 1
	SWY ♂	= 5
	(SWBr ♀	= 1)
	LWBr ♂	= 1

The expectation is as follows:

P_1	SWByX	– SWByX			
	I RYbX	– Yb			
Gametes of F_1	SWBYX	– SWByX	– LRYbX	– LRybX	Eggs
	LWBYX	– LWByX	– SRYbX	– SRybX	
	SWBYX	– SWByX	– Yb	– yb	Sperm

F_2	SWN ♀	3	SWN ♂	3
	LRN ♀	3	LWN ♂	3
	SWB ♀	1	LRY ♂	3
	LRB ♀	1	SRY ♂	3
	SRN ♀	3	SWB ♂	1
	LWB ♀	1	LWB ♂	1
	LWN ♀	3	LRBr ♂	1
	SRB ♀	1	SRBr ♂	1

There are seven cases of crossing-over in color. In addition there is one record of SWBr ♀ which must be either an error, or a mutation, since both the female-producing sperm carry the factor for black, hence no brown females are possible. Omitting this single case there are seven cases of crossing-over in 1611 males. Of these one is one way (RB), and six in the opposite

direction. The recessive RB combination may be obscured by the red, normal or black, female classes.

Concerning the cases of crossing-over for character of wing SWN ♂ = 418, while LWN ♂ = 224; SWR ♂ = 145, while LWB ♂ = 95. On the other side, LRY ♂ = 419, while SWY ♂ = 161; LRBr ♂ = 102, while SRBr ♂ = 47. The sum of the 'straight' males is 1081, and that of the cross-overs 527; or almost exactly 2 to 1.

The reciprocal cross is as follows:

SWB ♂ by LRY ♀

LRN ♀ = 121
LRY ♂ = 76

F_2	LRN ♀ = 808 LRB ♀ = 215 LWN ♂ = 191 LWB ♂ = 63 SWN ♂ = 221 SWB ♂ = 108 LRY ♀ = 442 LRY ♂ = 335 LRBr ♀ = 76 LRBr ♂ = 73 SRY ♂ = 118 SRBr ♂ = 17

The analysis follows:

P_1	LRYbX – LRYbX SWByX – ...yb	
Gametes of F_1	LRbyX – LRYbX – SWByX – SWBYX SRbyX – SRYbX – LWByX – LWBYX	Eggs
	LRbyX – LRYbX – ...yb – ....Yb	Sperm
F_2	LRBr ♀ = 2 LRY ♀ = 6 LRB ♀ = 2 LRN ♀ = 6	LRBr ♂ = 1 SRBr ♂ = 1 LRY ♂ = 3 SRY ♂ = 3 SWB ♂ = 1 LWB ♂ = 1 SWN ♂ = 3 LWN ♂ = 3

Despite the large number of individuals (2677), there are no cases of crossing-over for color in the last case. If such occurred in the females, they would be masked by the presence of the dominant factor, R, present in all female-producing sperm. Concerning the crossing-over of wing characters, it will be noted that LRY ♂ = 335, while SRY ♂ = 118; and LRBr ♂ = 73, while SRBr ♂ = 17; and the on other hand, SWB ♂ = 108, while LWB ♂ = 63 and SWN ♂ = 221, while LWN ♂ = 191. The sum of the 'straight' cases is 737, while that of the cross-overs is 398, or approximately 2 to 1.

LONG, RED, BLACK BY SHORT, WHITE, YELLOW

When LRB females are paired with SWY males, the offspring are LRN ♂'s and ♀'s. The second generation is given below:

LRB ♀ by SWY ♂

F_1	LRN ♀ 94 LRN ♂ 111
F_2	LRN ♀ = 1819 LRN ♂ = 562 LRB ♀ = 463 LRB ♂ = 163 LWY ♂ = 279 LWBr ♂ = 78 SWBr ♂ = 194 SWY ♂ = 371 SRN ♂ = 266 SRB ♂ = 53 LWN ♂ = 3 LRY ♂ = 3 LRBr ♂ = 1 (LRY ♀ = 3)

The expectation is as follows:

P_1	LRByX – LRByX SWYbX – ...Yb

Gametes of F_1	LRBYX	–	LRByX	–	SWYbX	–	SWybX	} Eggs
	SRBYX	–	SRByX	–	LWYbX	–	LWybX	
	LRBYX	–	LRByX	–	....Y	–	.....y	Sperm

F_2	LRN	♀ 12	LRN	♂ 3
	LRB	♀ 4	SRN	♂ 3
			SWY	♂ 3
			LWY	♂ 3
			LRB	♂ 1
			SRB	♂ 1
			SWBr	♂ 1
			LRBr	♂ 1

There were seven cases of crossing-over in 1466 males, and three cases in 2282 females. In the males the three crossings in one direction (LWN) are balanced by four crossings in the other direction (LRY, and LRBr). The three cases in the females (LRY) can not be explained by crossing-over in the eggs, since all female-producing sperms carry the factor for black, hence no yellow females are possible, unless one of these sperms should lose the B factor, which would be a mutation. Hence the case is due either to this, or to some error.

In the wing characters we find LRN ♂ = 562, while SRN ♂ = 266; LRB ♂ = 163, while SRB ♂ = 53. On the other hand, SWY ♂ = 371, while LWY ♂ = 279; SWBr ♂ = 184, while LWBr ♂ = 78. The sum of the 'straight' males is 1280, and the cross-overs 676, a ratio of about 2 : 1.

The reciprocal cross gave the following results:

LRB ♂ by SWY ♀

F_1	LRN ♀	83
	SWY ♂	79
F_2	LRN ♀	= 355
	LRN ♂	= 301
	LRB ♀	= 90
	LRB ♂	= 90
	LWY ♀	= 164
	LWY ♂	= 116
	LWBr ♀	= 35
	LWBr ♂	= 36
	SWY ♀	= 147
	SWY ♂	= 174
	SWBr ♀	= 50
	SWBr ♂	= 48
	SRN ♀	= 140
	SRN ♂	= 150
	SRB ♀	= 41
	SRB ♂	= 36
	SWN ♂	= 2
	LWN ♂	= 5
	LRY ♂	= 3
	SWN ♀	= 2
	LWN ♀	= 9 (in one bottle)

The expectation is as follows:

P_1 .	SWYbX	– SWYbX			
	LRByX	– ...by			
Gametes of F_1	SWbyX	– SWbYX	– LRByX	– LRBYX	Eggs
	LWbyX	– LWbyX	– SRByX	– SRBYX	
	SWbyX	– SWYbX	– ...by	– ...bY	Sperm

F_2	SWB ♀	= 1	SWBr ♂	= 1	
	LWB ♀	= 1	LWBr ♂	= 1	
	SWY ♀	= 3	SWY ♂	= 3	
	LWY ♀	= 3	LWY ♂	= 3	
	LRB ♀	= 1	LRB ♂	= 1	
	SRB ♀	= 1	SRB ♂	= 1	
	LRN ♀	= 3	LRN ♂	= 3	
	SRN ♀	= 3	SRN ♂	= 3	

There were ten cases of crossing-over in 951 males, and eleven cases in 1022 females. In the former there were seven cases in one direction (SWN and LWN) balanced by only three cases in the opposite direction (LRY); but the latter are known to be less viable. In the females the eleven cases were in the same direction (SWN and LWN). Of these nine occurred in one bottle, suggestive of some error.

In wing characters there were LRN ♂ 301, while SRN ♂ = 150; LRB ♂ = 90, while SRB ♂ = 36; on the other hand, SWY ♂ = 174, while LWY ♂ = 116; SWBr ♂ = 48, while LWR ♂ = 36. The sum of the 'straight' males is 613, and the cross-overs 332, approximately 2 to 1.

SHORT, RED, BLACK BY LONG, WHITE, NORMAL

When females SRB are mated to LWN, the female offspring are LRN, and the males SRN. The second generation is given below:

SRB ♀ by LWN ♂

F_1	LRN ♀	195
	SRN ♂	147
F_2	LRN ♀	= 885
	LRN ♂	= 316
	LRB ♀	= 215
	LRB ♂	= 94
	LWN ♂	= 410
	LWB ♂	= 130
	SRN ♀	= 482
	SRN ♂	= 572
	SRB ♀	= 151
	SRB ♂	= 198
	SWN ♂	= 166
	SWB ♂	= 51

The expectation is as follows:

P_1	SRByX	– SRByX
	LWBYX	– ...bY

Gametes of F_1	SRBYX – SRByX – LWBYX – LWByX LRBYX – LRByX – SWBYX – SWByX	Eggs	
	SRBYX – SRByX – ...bY – ...by	Sperm	
F_2	SRN ♀ 6	SRN ♂ 3	
	LRN ♀ 6	LRN ♂ 3	
	SRB ♀ 2	LWN ♂ 3	
	LRB ♀ 2	SWN ♂ 3	
		SRB ♂ 1	
		LRB ♂ 1	
		LWB ♂ 1	
		SWB ♂ 1	

There was no evidence of crossing of color factors in 1937 males, and none are expected, since both Black and Normal carry the black factor; and the yellow factor that distinguishes them is not sex-linked. In wing characters SRN ♂ = 572, while LRN ♂ = 316, SRB ♂ = 198, while LRB ♂ = 94. On the other hand, LWN ♂ = 410, while SWN ♂ = 166; LWB ♂ = 130, while SWB ♂ = 51. The sum of the 'straight' males is 1310 and the cross-overs 627, nearly 2 to 1.

The reciprocal cross is as follows:

SRB ♂ by LWN ♀

F_1	LRN ♀	514
	LWN ♂	404

F_2	LRN ♀	= 831	
	LRN ♂	= 312	
	LRB ♀	= 278	
	LRB ♂	= 78	
	LWN ♀	= 661	
	LWN ♂	= 616	
	LWB ♀	= 189	
	LWB ♂	= 184	
	SRN ♂	= 282	
	SRB ♂	= 146	
	SWN ♂	= 244	
	SWB ♂	= 89	
	(SWN ♀	= 5)	(in one bottle)

The expectation is as follows:

P_1	LWBYX	– LWBYX			
	SRByX	– ...by			
Gametes of F_1	LWByX	– LWBYX	– SRByX	– SRBYX	Eggs
	SWByX	– SWBYX	– LRByX	– LRBYX	
	LWByX	– LWBYX	– ...by	– ....Y	Sperm

F_2	LWB	♀ 2	LWB	♂ 1	
	LWN	♀ 6	SWB	♂ 1	
	LRB	♀ 2	LWN	♂ 3	
	LRN	♀ 6	SWN	♂ 3	
			SRB	♂ 1	
			LRB	♂ 1	
			SRN	♂ 3	
			LRN	♂ 3	

There were 5 SWN ♀'s, all from one bottle; which can not be explained by crossing-over. They are either mutations or due to error.

Concerning wing-characters, SRB ♂ = 146, while LRB ♂ = 78; SRN ♂ = 282, while LRN ♂ = 312. On the other hand, LWN ♂ = 616, while SWN ♂ = 244; LWB ♂ = 184, while SWB ♂ = 89. The sum of the 'straight' males is 1228, while that of the cross-overs is 721. The 'straights' are less than twice the cross-overs, due largely to the SRN's being actually less than the LRN's.

CONCLUSION

The principal object of the preceding experiments was to study the phenomenon of linkage on a relatively large scale. The results show that whatever sex-linked factors enter into combination, those factors come out together in the grandchildren. Moreover, it makes no difference from the point of view of linkage whether a 'present' factor is linked to another 'present' factor or to an 'absence,' or even whether two absences are linked together in one of the parents. The phenomenon is the same, as both Bateson and I have pointed out.[2] The results are the more striking when

[2] This statement is too sweeping in so far as based on the evidence given in the text.

it is found in the same experiments that other factors not showing sex-linked inheritance do not show associative inheritance with those factors that are sex-linked. It is here that the chromosomal hypothesis seems to give an insight into the nature of the difference in the two cases.

In those counts where crossing-over in color is expected there were 61 such cases in a total of 12115; a gametic ratio of 1 to 198. The crossing-over is such a rare occurrence that although the total number of individuals is large, it is by no means large enough to make the ratio significant.

On the other hand, where the gametic ratio for crossing is low, as in the wing-characters, the numbers suffice to make the values significant, and it will be observed how closely these approximate 1 to 2. Moreover, the crossings balance quite well the counter-crossings, which is expected on the theory of chromosomal interchanges.

The same balance is expected for the color ratio but here we find, as the following table shows, that 18 crossings were in one direction and 43 in the other:

RB	Wb		
4	1		
0	0	in	260
WB	Rb		
5	0	in	337
9	0	in	1477
WB	Rb		
3	4	in	872
RB	Wb		
1	6	in	1611
0	0	in	1126
WB	Rb		
3	4	in	1466
1	3	in	1973
43	18		12115

But these numbers are, as stated, too small to be significant. It should be noted that no *actual* exchanges between the eggs them-

selves are expected, since one of the exchanges always goes into the polar body; but on an average the loss to the polar body should be as often of one kind as of the other. In order to test this more fully the 'exchanges' should be equally viable, which is not the case in the present experiments, where a correction for viability has to be supplied.

It will be noted that the few cases, in which impossible female classes appear, have been 'explained away' as due to mutation or to error. We believe that we are justified in making this assumption on the basis of our general knowledge of the behavior of these factors in heredity and of the possible experimental errors. But a critic will not be slow in pointing out that these cases can be explained if crossing-over is admitted for the male. The fairness of this criticism must be admitted. Whether it is justified, further work must show, and this work is under way.