TWO SEX-LINKAGES IN THE HOUSE MOUSE, WITH UNUSUAL RECOMBINATION VALUES

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IN 1945, in Line Thirteen of the series of inbred lines set up by Professor R. A. Fisher in the house mouse, *Mus musculus*, a disturbed segregation of shaker (sh_2) and sex was noticed. Data collected from three unrelated lines, Eight, Twelve and Eighteen, in which wavy (wv_2) and shaker (sh_2) were segregating, indicated linkage between these two factors and sex. G. D. Snell and L. W. Law (1939) had published data from which a crossover value of 25 per cent. between wavy and shaker had been obtained. An experiment was therefore set up, designed to investigate their linkage relations not only with each other but also with sex.

Appropriate genotypes were taken from Lines Twelve and Eighteen and a separate stock of wavy and shaker ; crosses were made to produce each of the four kinds of males needed.

(i) Tricoupling $\quad ♂ \dfrac{wv_2\ sh_2\ X}{+\ \ +\ Y}$

(ii) wv_2 and sh_2 in coupling $\quad ♂ \dfrac{wv_2\ sh_2\ Y}{+\ \ +\ X}$

(iii) sh_2 and sex in coupling $\quad ♂ \dfrac{+ sh_2\ X}{wv_2 + Y}$

(iv) wv_2 and sex in coupling $\quad ♂ \dfrac{wv_2 + X}{+ sh_2\ Y}$

In order that any causes other than linkage, likely to disturb the ratios obtained, should be distributed at random throughout the matings, mates were chosen during the following generations without regard to their consanguinity. Approximately a hundred mice were bred from each type of triple backcross (comprising twenty-four matings). The results are tabulated by phenotypes on page 350 (table 1).

In a form more convenient for considering linkage relations, these data may be tabulated as under, the columns representing respectively :

I. Parental types.
II. Recombinants, with crossovers interchanging X and Y.

TABLE I

(i) ♀ $\frac{wv_2sh_2\,X}{wv_2sh_2\,X}$ × ♂ $\frac{wv_2sh_2\,X}{+\,+\,Y}$

Mating	♀♀ wv_2sh_2	♀♀ wv_2	♀♀ sh_2	♀♀ +	♂♂ wv_2sh_2	♂♂ wv_2	♂♂ sh_2	♂♂ +	Total
3	3	3	1	2	4	...	1	1	15
7	2	3	1	5	1	...	1	...	13
11	...	2	...	4	1	2	...	...	9
12	...	...	...	1	2	...	1	...	4
18	1	...	1	2	2	...	1	4	11
19	2	2	2	7	2	1	...	3	19
25	1	1	1	2	1	1	...	1	8
28	2	1	1	1	2	2	...	...	9
36	2	4	1	4	1	4	1	1	18
...	13	16	8	28	16	10	5	10	106

(ii) ♀ $\frac{wv_2sh_2\,X}{wv_2sh_2\,X}$ × ♂ $\frac{wv_2sh_2\,Y}{+\,+\,X}$

Mating	♀♀ wv_2sh_2	♀♀ wv_2	♀♀ sh_2	♀♀ +	♂♂ wv_2sh_2	♂♂ wv_2	♂♂ sh_2	♂♂ +	Total
4	8	2	2	5	6	1	2	4	30
8	1	...	1	1	2	...	2	3	10
16	2	1	...	1	4	...	2	3	13
24	13	1	...	9	7	4	3	12	49
27	...	1	...	...	...	...	1	2	4
34	5	1	3	1	...	1	1	2	14
...	29	6	6	17	19	6	11	26	120

(iii) ♀ $\frac{wv_2sh_2\,X}{wv_2sh_2\,X}$ × ♂ $\frac{+sh_2\,X}{wv_2+\,Y}$

Mating	♀♀ wv_2sh_2	♀♀ wv_2	♀♀ sh_2	♀♀ +	♂♂ wv_2sh_2	♂♂ wv_2	♂♂ sh_2	♂♂ +	Total
6	4	4	1	3	...	5	4	...	21
13	3	10	6	5	7	7	9	4	51
21	1	5	3	3	3	5	6	2	28
22	1	2	3	...	...	1	1	...	8
33	1	1	6	1	1	2	4	3	19
...	10	22	19	12	11	20	24	9	127

(iv) ♀ $\frac{wv_2sh_2\,X}{wv_2sh_2\,X}$ × ♂ $\frac{wv_2+X}{+\,sh_2\,Y}$

Mating	♀♀ wv_2sh_2	♀♀ wv_2	♀♀ sh_2	♀♀ +	♂♂ wv_2sh_2	♂♂ wv_2	♂♂ sh_2	♂♂ +	Total
5	3	2	7	...	1	8	9	2	32
9	3	2	...	1	1	5	4	3	19
17	2	2	6	4	3	7	7	1	32
20	1	1	5	2	3	2	2	1	17
...	9	7	18	7	8	22	22	7	100

III. Recombinants, with crossovers interchanging wv_2 and its normal allelomorph.

IV. Recombinants, with crossovers interchanging sh_2 and its normal allelomorph.

TABLE 2

Observed (m+x)

	Paternal types	Recombinants				Totals
		I	II	III	IV	
		—	X	wv_2	sh_2	
(i) Tricoupling	♂ $\frac{wv_2 sh_2\ X}{+\ +\ Y}$	23	44	18	21	106
(ii) wv_2—sh_2 in coupling . . .	♂ $\frac{wv_2 sh_2\ Y}{+\ +\ X}$	36	55	17	12	120
(iii) sh_2—sex in coupling . . .	♂ $\frac{+ sh_2\ X}{wv_2 +Y}$	39	46	19	23	127
(iv) wv_2—sex in coupling . . .	♂ $\frac{wv_2 +X}{+ sh_2\ Y}$	29	40	15	16	100
	Totals . .	127	185	69	72	453

It will be seen that this table involves the grouping of data concerning pairs of complementary genotypes from each kind of mating, these pairs being arranged as are the letters in a symmetrical 4×4 Latin Square. If there are any viability differences they may normally be expected to show most plainly between the members of these pairs. A χ^2 test on their approximation to 1 : 1 ratios will indicate if any of these pairs of genotypes are unequally viable (table 3).

TABLE 3

Pairs of complementary genotypes	Totals	χ^2
$wv_2 sh_2$ ♀ 61 + + ♂ 52	113	0·7168
+ + ♀ 64 $wv_2 sh_2$ ♂ 54	118	0·8475
+ sh_2 ♀ 51 wv_2 + ♂ 58	109	0·4495
wv_2 + ♀ 51 + sh_2 ♂ 62	113	1·0708
	453	3·0846 ; n=4

The low χ^2 indicates that there are no obvious viability disturbances.

A further and more comprehensive test, to discern whether viability or any other factors are disturbing the data, may be made by comparing the observed frequencies with those expected on the basis of the marginal totals in table 2 (table 4) :

TABLE 4

(a) *Expected* (m)

	I	II	III	IV	
(i)	29·7174	43·2892	16·1457	16·8477	106·0000
(ii)	33·6424	49·0066	18·2781	19·0729	120·0000
(iii)	35·6049	51·8653	19·3444	20·1854	127·0000
(iv)	28·0353	40·8389	15·2318	15·8940	100·0000
	127·0000	185·0000	69·0000	72·0000	453·0000

(b) (x^2/m)

	I	II	III	IV	Total χ^2
(i)	1·5184	0·0117	0·2130	1·0234	
(ii)	0·1652	0·7330	0·0894	2·6229	
(iii)	0·3237	0·6633	0·0061	0·3925	
(iv)	0·0332	0·0172	0·0035	0·0071	
	2·0405	1·4252	0·3120	4·0459	7·8236 ($n=9$)

The χ^2 is again insignificant for these nine degrees of freedom.

Finally, any inequality due to viability or other factors between the four pairs of genotypes in table 3, which might have disturbed the linkage relations, will become evident by comparison with the expected frequencies of these genotypes ; these can be drawn from table 4*a* and appear below, together with a χ^2 test comparing them (table 5) :

TABLE 5

Genotypes	Expected (m)	Observed (m+x)	x^2/m
wv_2sh_2 ♀♀ and + + ♂♂	113·9624	113	0·00813
+ + ♀♀ and wv_2sh_2 ♂♂	112·3488	118	0·28426
+ sh_2 ♀♀ and wv_2+♂♂	111·6624	109	0·06348
wv_2 + ♀♀ and + sh_2♂♂	115·0264	113	0·03570
	453·0000	453	0·39157 ($n=3$)

The χ^2 is extremely low, and contributes very little to the total χ^2 of 7·8236 for nine degrees of freedom (in table 4*b*).

It appears, therefore, that viability and other disturbances are negligible.

It remains to test the hypothesis of independent segregation of sex with shaker and wavy. A χ^2 test on the approximation to a 1 : 1 ratio of the parental types of offspring against the recombinants involving an interchange of *X* and *Y* is given below :

Parental types	Recombinants	χ^2	
127	185	10·782	($n=1$)

The value of χ^2 for one degree of freedom is equivalent to a normal deviate of 3·284 standard deviation ; the one in 1000 level of significance requires 3·241. The hypothesis of independence is therefore untenable.

It is reasonable, therefore, to conclude that the factors wavy and shaker are linked, not only with each other, but also with sex. The recombination values derived from table 2 are (table 6) :

TABLE 6

Linked loci	Recombinants	Total	Percentage recombination	Standard error
wv_2 and sh_2	69+72=141	453	31·06 per cent.	2·174 per cent.
wv_2 and sex	185+69=254	453	56·07 ,,	2·332 ,,
sh_2 and sex	185+72=257	453	56·73 ,,	2·328 ,,

The recombination value between shaker and wavy is higher than that found by Snell and Law (1939). However, their estimate was based principally on female gametogenesis, and that given above is based on male gametogenesis ; it is not impossible, therefore, that they should differ. For males, Snell and Law report 15 recombinants out of 56, an observation not incompatible with a recombination value exceeding 30 per cent.

The two main conclusions to be drawn from table 6 are : first, that the recombination values between shaker and sex and between wavy and sex are both significantly greater than 50 per cent. ; and, secondly, that the two loci, wavy and shaker, recombination between which is as great as 31 per cent., are nevertheless similarly related as regards their values with sex.

Explanation of these phenomena is outside the scope of this paper, but it is submitted that while these conclusions appear mutually repugnant, the data given above supply very strong evidence for each of them.

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REFERENCE

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