LOCATION OF " REELER " IN LINKAGE GROUP III OF THE MOUSE

D. S. FALCONER

Animal Breeding and Genetics Research Organisation,
Institute of Animal Genetics, Edinburgh, 9

" REELER " (rl) is a recessive gene of the house mouse which impairs locomotion through a disturbance of balance. It has been tested for linkage with a few markers, with which it was found to segregate independently (Falconer, 1951). The loci of macrocytic anæmia (W) and of luxate (lx), in linkage group III were, however, not included in these tests, and subsequent work has shown reeler to be linked with these two loci, the order being $W-lx-rl$, and the recombination 16 per cent. with lx and 29 per cent. with W. This linkage is interesting in that it adds another 16 units to this already long linkage group, but its practical value in linkage studies is not likely to be great on account of the poor breeding performance of reeler homozygotes. On the other hand the linkage may have some value as an aid in the maintenance of reeler stocks.

The data which give evidence of the linkage come from four types of mating, of which the parental genotypes are shown in table 1. The viable allele of macrocytic anæmia (W^v) was used in the tests. Some of the matings segregated all three loci, but in the presentation and analysis of the data the two tests, rl with W^v and rl with lx, are treated separately. Reeler segregated always from an intercross ; the other loci segregated either from an intercross or a backcross, and in each case the coupling and repulsion phases were represented, though not always equally. The distribution of the progeny of each type of mating among the different phenotypic classes is given in table 1.

The analysis of the data was made by means of Fisher's scoring system (Fisher, 1946), and the scores (S) and amounts of information (I) for each type of mating are set out in table 2. The columns headed 1 are based on scoring coefficients calculated for the assumption of free recombination $(p = 0.5)$ and undisturbed single-factor segregations. The highly significant values of χ^2 disprove the hypothesis of independent segregation beyond doubt, and the analyses indicate approximate recombination fractions of 35 per cent. with W^v and 25 per cent. with lx.

The more precise estimation of the recombination fractions is complicated by the faulty single-factor segregations of both W^v and lx. There is a deficiency of $W^v W^v$ phenotypes which may be attributed

to prenatal mortality, and a deficiency also of *lxlx* phenotypes which may be attributed, in part at least, to linkage in coupling with W^v.

TABLE 1

Observed segregation of rl *with* W^v *and with* lx

Type of mating	Genotype of		+			rl			Total
	Female	Male	W^vW^v	W^v+	$++$	W^vW^v	W^v+	$++$	
A	$\dfrac{W^v+}{+rl}$	$\dfrac{W^v+}{+rl}$	6	22	11	2	4	9	54
B	$\dfrac{W^vrl}{++}$	$\dfrac{W^vrl}{++}$	13	85	33	10	12	2	155
C	$\dfrac{+rl}{++}$	$\dfrac{W^v+}{+rl}$	...	13	7	...	2	8	30
D	$\dfrac{+rl}{++}$	$\dfrac{W^vrl}{++}$	...	33	51	...	13	11	108
			lxlx	*lx+*	$+$	*lxlx*	*lx+*	$+$	
A	$\dfrac{lx+}{+rl}$	$\dfrac{lx+}{+rl}$	10	41	19	2	2	25	99
B	$\dfrac{lx\,rl}{++}$	$\dfrac{lx\,rl}{++}$	7	22	61	7	1	5	103
C	$\dfrac{lx+}{+rl}$	$\dfrac{++}{+rl}$	...	14	29	...	0	6	49
D	$\dfrac{lx\,rl}{++}$	$\dfrac{+rl}{++}$	...	9	32	...	3	8	52

In addition, *lx* shows normal overlapping of the heterozygote class. In order to make allowance for these disturbed segregations the scoring coefficients were recalculated on the basis of the observed frequencies of the W^vW^v, *lxlx*, and *lx+* phenotypic classes. Thus the expected frequencies for the single-factor segregations were as follows : for intercrosses,

Phenotype   . . W^vW^v W^v+ $++$ *lxlx* *lx+* $\overbrace{\qquad+\qquad}$

$\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad lx+\quad ++$

Expectation .   . 0·15 0·56 0·29 0·13 0·32 0·26 0·29

and for luxate in backcrosses,

Phenotype   . . *lx+* $\overbrace{\qquad+\qquad}$

$\qquad\qquad\qquad\qquad\qquad\qquad\qquad lx+\quad ++$

Expectation   . . 0·26 0·24 0·50

The recombination values assumed in the re-scoring were those indicated by the first analysis, 35 per cent. with W^v and 25 per cent. with *lx*. The scores and information obtained with the revised coefficients are given in the columns headed 2 in table 2. The

estimates of the recombination fractions are now substantially lower than those obtained from the first analysis, 30 per cent. with W^v and 16 per cent. with lx, the reduction being due to the removal

TABLE 2

Analysis of the data in table 1

Type of mating	W^v						lx					
	1 ($p = 0.50$)		2 ($p = 0.35$)		3 ($p = 0.30$)		1 ($p = 0.50$)		2 ($p = 0.25$)		3 ($p = 0.15$)	
	S	I	S	I	S	I	S	I	S	I	S	I
A	21	144	0	161	−10	188	80	264	28	178	11	263
B	59	413	34	410	21	463	80	275	19	309	−16	514
C	16	40	9	43	7	46	2	65	4	34	4	51
D	16	144	−5	155	−13	165	5	69	−3	22	−5	22
Total . .	112	741	38	769	5	862	167	673	48	543	−6	850
χ^2 . .	17		1.9		0.025		41		4.2		0.04	
Estimated recombination	35%		30%		29%		25%		16%		16%	
Standard error	...		...		3.4%		...		...		3.4%	

S = Score. I = Amount of information.

of the disturbing effects of the aberrant single-factor segregations. A third analysis based on the revised recombination fractions was made, and the results are given in the columns headed 3 in table 2. The values of χ^2 testing deviation from the assumed recombination fractions are now very small, and the final estimates of recombination with their standard errors are

$$W^v-rl : p = 29 \pm 3.4 \text{ per cent.}$$
$$lx \ -rl : p = 16 \pm 3.4 \text{ per cent.}$$

These values accord well with the recombination of 17.7 ± 1.2 per cent. observed for W^v with lx (Carter, 1951), and the order of the three loci is proved to be $W^v-lx-rl$.

REFERENCES

CARTER, T. C. 1951. The genetics of luxate mice. II. Linkage and independence. *J. Genet.*, *50*, 300-306.

FALCONER, D. S. 1951. Two new mutants, " Trembler " and " reeler," with neurological actions in the house-mouse (*Mus musculus*, L.). *J. Genet.*, *50*, 192-201.

FISHER, R. A. 1946. A system of scoring linkage data, with special reference to the pied factors in mice. *Amer. Nat.*, *80*, 568-578.