

GENETIC STUDIES IN POULTRY  
X. LINKAGE DATA FOR THE SEX CHROMOSOME

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LINKAGE DATA

FOR some years past I have been accumulating data in connexion with the topography of the sex-chromosome in the fowl. Though most of the experiments made during this time were mainly designed for other purposes, they were so framed as to allow of the estimation of various linkages between certain genes in the sex-chromosome. In this way has been got together the considerable body of data given in Section A of the Appendix. As Hutt (1936) has recently pointed out, there is now evidence for the existence of seven sex-linked genes, and for these he has furnished a tentative map. My own data are concerned with but four of these genes, viz. those for silver, slow feathering, barring and light shank. On the whole, the fresh data that I have to offer are in general accordance with those of earlier observers which are given in Section B of the Appendix. Of the four genes with which we are dealing there is a fairly close linkage between silver (**S**)<sup>1</sup> and slow feathering (**K**), while between silver and barring (**B**) and between silver and the shank pigment inhibitor (**Id**) there is a high percentage of cross-overs (*cr.*), as also between **B** and **K**. This is shown below in the data condensed from both sections of the Appendix, and these hardly call for further comment.

*Condensed data*

	Coupling				Repulsion				<i>cr.</i>	<i>cr. value</i>
									<i>ncr.</i>	
<b>S</b> and <b>Id</b>	157	171	145	177	53	108	91	75	474 533	47.07
<b>S</b> and <b>B</b>	180	143	140	177	205	176	184	192	680 717	48.68
<b>K</b> and <b>Id</b>	113	90	97	111	124	105	122	70	381 451	45.79
<b>K</b> and <b>S</b>	603	94	159	648	12	24	26	9	274 1301	17.39
<b>K</b> and <b>B</b>	374	273	272	293	110	116	116	117	772 899	46.20
<i>Note.</i> McArthur's data are not included in the above since he does not separate his material into 4 classes, giving only the number of cross-overs as compared with that of non-crossovers. But where the data relate to the above four genes they have been included opposite, and the figures revised.									642	47.06
									722	
									566 657	46.28
									333 1821	15.46

<sup>1</sup> Throughout I have made use of the symbols given in Hutt's indispensable little paper.

There remains, however, for discussion the relation between **B** and **Id**. Barred birds, as is well known, always have light shanks, since the factor which brings about the barring of the plumage also inhibits the development of mesodermal pigment in the shanks just as does **Id**. This renders it difficult to obtain linkage data for this pair of genes, a fact recognized by all observers who have worked with them. Hutt, though I am not clear upon what authority, states that "barring and the inhibitor of dermal pigments are so closely linked that only two doubtful cross-overs between them have been reported". On the other hand, Serebrovsky (1930) gives some experimental data indicating a linkage not nearly so close. His method was to use males heterozygous for **B** and **Id**, mating them with non-barred dark-shanked females. The barred offspring are neglected since they are light-shanked whether they contain **Id** or not. The proportion of light- and dark-shanked birds among the unbarred offspring then affords a measure of the linkage, it being known whether the gametic output of the male is of the coupling or repulsion type. Among fifty birds so bred Serebrovsky obtained eight cr. and estimated the cr. value to be  $16 \neq 5$ . I have also made an experiment of a similar nature. In 1934 I crossed a Barnevelder hen with a Cambar male and subsequently mated one of the barred cocks so bred with unbarred dark-shanked hens. The barred Cambar does not contain **Id**, resembling in this respect the Campine on which the breed was founded; but this factor was brought into the cross by the Barnevelder hen. Constitutionally therefore the  $F_1$  male was **Bid/bId**. If there is a fairly close linkage between **B** and **Id** we should expect the great majority of his unbarred gametes to carry **Id**, and consequently a great excess of light-shanked birds in the unbarred class. Actually out of sixty-eight such birds twenty-eight had light shanks and forty had dark. This result is utterly at variance with Serebrovsky's, and the only suggestion I can offer is that we are here dealing either with a genetically distinct shank inhibitor, or else with **Id** which has become dislocated on to an autosome.

On the other hand, I am able to bring forward some entirely different evidence of a positive nature. In 1926 a cross was made between a White Wyandotte hen and an Indian Game cock. The hen unexpectedly turned out to be carrying barring which she doubtless owed to one or more crosses in the history of her progenitors. From what follows it may be taken that she did not carry **Id**, which was brought into the cross by the Indian Game male. On this supposition the  $F_1$  males were constitutionally **Bid/bId**. In 1927 and 1928 two of them were mated with a number of white silky hens, all with the characteristic development of

mesodermal pigment. The chicks on hatching showed a very sharp distinction between those with dark and those with light shanks, and this was equally true for the whites and well as for the various colour classes which appeared. As they developed it was found that nearly all of those which hatched with dark shanks became barred birds, though as they grew older the shanks became light. The bulk of the unbarred birds had light shanks, but the few that started with dark shanks remained dark. The proportion in which the different classes occurred is shown below:

Silver barred dark	30
„ light	2
Silver unbarred dark	1
„ light	23
Gold barred dark	18
„ light	—
Gold unbarred dark	6
„ light	17
White* dark	28
„ light	31

\* Not all of the whites were recorded. The experiments formed part of a series made by Mr M. S. Pease and myself to test for the existence of a sex-linked factor affecting fecundity. For this the whites were valueless and consequently often rejected on hatching.

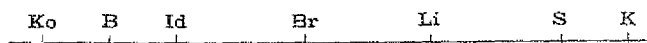
The natural explanation is that in repressing the mesodermal shank pigment the barring factor comes into action later than does the inhibitor. Where a chick hatches with light shanks and subsequently becomes a barred bird this is because it contains **Id** as well as **B**. On the other hand, unbarred birds with dark shanks are those containing neither **B** nor **Id**. Of the whites we can say nothing as to the barring factor though it is clear that about half contain **Id** and half do not. If we arrange our coloured birds with respect to **B** and **Id** we obtain the following numbers for our four classes:

<b>BId</b>	<b>Bid</b>	<b>bId</b>	<b>bid</b>
2	48	40	7

with a cr. value of 9.3%. This value is somewhat lower than that obtained by Serebrovsky, but far from the very close linkage suggested by Hutt. For the present I propose that the cr. value for **B** and **Id** be regarded as somewhere about 10. The figure is admittedly a rough approximation only, and in view both of the paucity of data and of the anomalous result from the Barnevelder-Cambar cross it is very desirable to test the matter by further experiment. The provisional fixing of this value for **B** and **Id** means a slight alteration in Hutt's tentative map, and the various facts can be best covered by locating **Id** fairly close to **B** on the side away from **Ko**, i.e. between **B** and **Br**. This position agrees with the linkage values

for **B**Li and **I**dLi respectively. More light will be thrown upon the case when we have some data relating **B** to **Br**.

The tentative map of the chromosome thus becomes as below:



The various cr. values are conveniently given in the appended scheme, and it will be seen that the figures are on the whole consistent.

	K	S	Li	Br	Id	B	Ko
K	*	15	24	42	46	46	47
S	15	*	16	44	47	48	50
Li	24	16	*	—	30	40	47
Br	42	44	—	*	27	—	—
Id	46	47	30	27	*	10	—
B	46	48	40	—	10	*	13
Ko	47	50	47	—	—	13	*

Passing from **K** to **Ko**, for example, the figures become progressively higher as expected. There are discrepancies here and there, as where the **BS** value is greater than the **BK** value, whereas the reverse should be the case. But such discrepancies only occur where the cr. value is very high, and in any case they are not marked.

#### IRREGULARITIES IN DATA.

Every observer who has collected data of the kind given here must have been struck by the marked irregularities which often occur even when considerable numbers are bred from similar material. An extreme case is that of Warren's figures for the **KS** linkage (see Appendix B). One cannot help feeling that there must be some specific reason why, in a total of 576 birds, one of the cr. classes should be barely one-fifth of the other where expectation was equality. The possibility of error in assignment does not enter here as it might in some cases where classi-

fication was difficult. No experienced observer could mistake a slow for a rapid feathering bird. Yet here it will be noticed that there are 351 rapids as against only 225 slows. The question arises whether we should continue to pool all data, trusting that irregularities will cancel out with the accumulation of large numbers; or whether we should found our cr. values on selected data with equal numbers of dominants and recessives and a homogeneous distribution of the cr. and non-cross-over (ncr.) classes. In this particular instance the inclusion or non-inclusion of Warren's data makes very little difference to the cr. values even though they form nearly a quarter of the material available. With his data the cr. value is 15.46, without it 15.90.

In connexion with irregularities there is one further point to be mentioned, viz. the possibility of cross-over ratios altering with age of parent. It was suggested by Haldane & Crew (1925) that this might occur in connexion with the **BS** linkage. It is a point that I have borne in mind during my work, and, as shown in Appendix A, several cocks have been tested for two or more years for the **BS** and for other linkages. The results offer no support to Haldane & Crew's suggestion.

#### DOUBLE CROSS-OVERS (DCR.)

The existence of dcr. in the sex-chromosome of the fowl was first pointed out by Serebrovsky & Wassina (1926), who, dealing with a case involving **Id**, **S** and **K**, obtained two such in forty-three birds. Further evidence of its existence was shortly afterwards given by Warren (1928). More adequate data were provided by Hertwig & Ritterhaus (1929). In an experiment involving **B**, **Li**, **S** and **K**, and comprising 104 birds, they found the percentage of dcr. to be 11.54%. In another experiment involving only **Li**, **S** and **K**, i.e. a much shorter portion of the chromosome, the percentage of dcr. was 4.43. They pointed out that these values are high, and offer evidence that the sex-chromosome is of considerable length.<sup>1</sup> In his valuable paper of 1933 MacArthur supplies a further case involving **Id**, **Br**, **S** and **K**, and comprising 272 birds. He found an even higher percentage of dcr. viz. 18.4, for this slightly shorter portion of the chromosome. Like Hertwig & Ritterhaus he also found an appreciable proportion of triple cross-overs (*circa* 2%), and like them concluded that the sex-chromosome must be a long one. To these cases I am now able to add a third one.

<sup>1</sup> In *Drosophila melanogaster*, where the chromosomes are few and relatively long, the dcr. value as worked out on a many point system is 7.53% for Chr. I and 6.42% for Chr. III. (Cf. Stern (1933).)

In 1937 a cross was made between a silver Wyandotte hen and a Legbar cock. Two of the males from this mating, in constitution **Bsk bSK**, were mated in 1938 and 1939 with **bsk** females. Determinations of the three characters were made on 315 offspring with the results shown below:

ner.		cr.				der.	
<b>K</b>	<b>k</b>	<b>K</b>	<b>k</b>	<b>K</b>	<b>k</b>	<b>K</b>	<b>k</b>
<b>S</b>	<b>s</b>	<b>s</b>	<b>S</b>	<b>S</b>	<b>s</b>	<b>s</b>	<b>S</b>
<b>b</b>	<b>B</b>	<b>B</b>	<b>b</b>	<b>B</b>	<b>b</b>	<b>b</b>	<b>B</b>
65	64	12	12	72	61	11	18
129		157				29	
=40.9%		49.9%				9.2%	

The proportion of der. is rather less than that found by Hertwig & Ritterhaus and only half of that found by MacArthur. But it must be remembered that these authors were dealing with a four-point linkage in which der. are more readily detected than in a three-point experiment such as mine. If MacArthur's case is treated as a three-point linkage involving only **Id**, **S** and **K** the percentage of der. works out at 4.1; and if that of Hertwig & Ritterhaus is similarly treated as involving only **B**, **S** and **K** the percentage of der. detectable drops from 11.5 to 5.8. Actually my own case points to an even higher proportion of der. than do the other two, and confirms the suggestion of these authors that we are evidently dealing with a very long chromosome. The conclusion is not without interest in view of the present controversy as to whether one of the two very long chromosomes or the much smaller V-shaped one is to be regarded as the sex-chromosome.

#### REFERENCES

- AGAR, W. E. (1924). *J. Genet.* **14**.  
 HALDANE, J. B. S. (1921). *Science*.  
 HALDANE, J. B. S. & CREW, F. A. E. (1925). *Nature, Lond.*, **115**.  
 HERTWIG, P. & RITTERHAUS, T. (1929). *Z. indukt. Abstamm.- u. VererbLehre*, **51**.  
 HERTWIG, P. (1930). *Biol. Zbl.* **50**.  
 HUTT, F. B. (1936). *Neue Forsch. in Tierzucht u. Abst.* (Duerst Festsch.).  
 MACARTHUR, J. W. (1933). *Genetics*, **18**.  
 SEREBROVSKY, A. S. (1922). *Amer. Nat.* **56**.  
 — (1926). *Genetics of Domestic Fowl*. Moscow.  
 SEREBROVSKY, A. S. & WASSINA, B. T. (1926). *J. Genet.* **17**.  
 SEREBROVSKY, A. S. & PETROV, S. G. (1930). *J. exp. Biol.* **6** (Russian).  
 STERN, C. (1933). *Faktorenkoppelung und Faktorenaustausch*. Berlin.  
 WARREN, D. C. (1928). *Genetics*, **18**.

Appendix A. *Own data*

S and Id:			Coupling				Repulsion				
Date	Pen. no.	♂ no.	Nature of ♂	SI <sub>d</sub>	Sid	sI <sub>d</sub>	sid	SI <sub>d</sub>	Sid	sI <sub>d</sub>	sid
1934	23	177	SI <sub>d</sub> /sid	6	12	6	4	—	—	—	—
1934	24	180	SI <sub>d</sub> /sid	—	—	—	—	5	10	2	7
1934	42	171	SI <sub>d</sub> /sI <sub>d</sub>	—	—	—	—	38	41	37	36
1935	42	171	"	—	—	—	—	22	42	38	21
1936	42	171	"	—	—	—	—	13	12	5	7
1934	43	169	SI <sub>d</sub> /sid	19	20	14	16	—	—	—	—
1937	20	169	"	25	33	17	40	—	—	—	—
1938	44	169	"	35	24	27	39	—	—	—	—
1938	45	511	"	40	39	43	46	—	—	—	—
Totals				125	128	107	145	78	105	82	71
				SB	Sb	sB	sb	SB	Sb	sB	sb
S and B:											
1927	43 + 45	235 244	SB/sb	17	13	3	12	—	—	—	—
1928	43 + 45	235 244		"	16	15	16	14	—	—	—
1929	24	178	Sb/sB	—	—	—	—	20	13	12	13
1930	24	178	"	—	—	—	—	14	19	20	19
1931	24	178	"	—	—	—	—	18	15	17	19
1932	24	178	"	—	—	—	—	15	15	24	21
1933	24	178	"	—	—	—	—	23	16	16	27
1936	22	401	SB/sb	16	21	19	30	—	—	—	—
1939	21	700	Sb/sB	—	—	—	—	30	21	30	26
1939	21	700	"	—	—	—	—	30	26	12	25
1939	22	657	"	—	—	—	—	35	31	29	20
Totals				49	49	38	56	185	156	160	170
				KI <sub>d</sub>	Kid	kI <sub>d</sub>	kid	KI <sub>d</sub>	Kid	kI <sub>d</sub>	kid
K and Id:											
1937	21	400	KI <sub>d</sub> /kid	15	9	12	12	—	—	—	—
1937	23	276	"	29	18	18	24	—	—	—	—
1937	24	532	"	6	5	3	5	—	—	—	—
Totals				50	32	33	41				
				KS	Ks	kS	ks	KS	Ks	kS	ks
K and S:											
1938	21	700	KS/ks	44	7	6	50	—	—	—	—
1939	21	700	"	39	5	17	32	—	—	—	—
1939	22	657	"	54	12	6	43	—	—	—	—
Totals				137	24	29	125				
				KB	Kb	kB	kb	KB	Kb	kB	kb
K and B:											
1938	21	700	Kb/kB	—	—	—	—	28	22	32	25
1939	21	700	"	—	—	—	—	21	23	21	28
1939	22	657	"	—	—	—	—	35	31	29	20
Totals								84	76	82	73

## Appendix B. Data from other observers

		SI <sub>d</sub>	Sid	sI <sub>d</sub>	sid	SI <sub>d</sub>	Sid	sI <sub>d</sub>	sid
<b>S and Id:</b>									
Hertwig (1930)	SI <sub>d</sub> /sid	32	39	36	30	—	—	—	—
Serebrovsky & Petrov (1930)	SI <sub>d</sub> /sid	—	4	2	2	—	—	—	—
"	Sid/sI <sub>d</sub>	—	—	—	—	5	3	9	4
	Totals	32	43	38	32	5	3	9	4
<b><sup>2</sup>S and B:</b>									
		SB	Sb	sB	sb	SB	Sb	sB	sb
Haldane (1921)	SB/sb	30	10	17	21	—	—	—	—
Agar (1924)	SB/sb	17	15	14	12	—	—	—	—
Serebrovsky & Wassina (1926)	SB/sb	21	13	13	14	—	—	—	—
"	Sb/sB	—	—	—	—	4	3	6	4
Hertwig & Ritterhaus (1929)	SB/sb	35	37	27	50	—	—	—	—
Hertwig (1930)	SB/sb	23	20	25	19	—	—	—	—
Serebrovsky & Petrov (1930)	SB/sb	5	0	6	5	—	—	—	—
"	Sb/sB	—	—	—	—	16	17	18	18
	Totals	131	94	102	121	20	20	24	22
<b>K and Id:</b>									
		KI <sub>d</sub>	Kid	kI <sub>d</sub>	kid	KI <sub>d</sub>	Kid	kI <sub>d</sub>	kid
Warren, 1928	KI <sub>d</sub> /kid	—	—	—	—	99	90	94	64
Serebrovsky & Wassina (1926)	KI <sub>d</sub> /kid	14	14	20	22	—	—	—	—
Hertwig (1930)	KI <sub>d</sub> /kid	36	25	27	31	—	—	—	—
Serebrovsky & Petrov (1930)	KI <sub>d</sub> /kid	13	19	17	17	—	—	—	—
"	kI <sub>d</sub> /KI <sub>d</sub>	—	—	—	—	25	15	28	6
	Totals	63	58	64	70	124	105	122	70
<b>K and S:</b>									
		KS	Ks	kS	ks	KS	Ks	kS	ks
Warren (1928)	KS/ks	211	14	68	283	—	—	—	—
Serebrovsky & Wassina (1926)	KS/ks	44	7	10	28	—	—	—	—
"	Ks/kS	—	—	—	—	3	9	10	1
Hertwig & Ritterhaus (1929)	KS/ks	152	16	31	142	—	—	—	—
Hertwig (1930)	KS/ks	33	12	10	41	—	—	—	—
Serebrovsky & Petrov (1930)	KS/ks	26	21	11	29	—	—	—	—
"	Ks/kS	—	—	—	—	9	15	16	8
	Totals	466	70	130	523	12	24	26	9
<b>K and B:</b>									
		KB	Kb	kB	kb	KB	Kb	kB	kb
Warren (1928)	Kb/kB	—	—	—	—	26	40	34	44
Serebrovsky & Wassina (1926)	KB/kb	54	40	43	52	—	—	—	—
"	"	195	125	135	141	—	—	—	—
Hertwig (1930)	"	71	55	53	41	—	—	—	—
Serebrovsky & Petrov (1930)	"	54	53	40	59	—	—	—	—
	Totals	374	273	272	293	26	40	34	44