

SEX-LINKED GENES IN THE FOWL

JOHN W. MACARTHUR
University of Toronto, Toronto, Ontario, Canada

Received November 12, 1932

INTRODUCTION

A study of the linkage relations obtaining among certain sex-linked genes of the fowl was begun by the author in 1925, the investigation having been first stimulated by PUNNETT's summary (1923) and the earlier work of GOODALE (1917), HALDANE (1921) and SEREBROVSKY (1922). After a preparatory detailed survey and several test matings of breeds to discover those containing the most favorable contrast of characters, chief attention was directed to reciprocal crosses between Columbian Plymouth Rocks and Gold Campines.

The former breed carries the dominant sex-linked genes for silver, slow feathering, light shank color, and light eye color, and lacks the barring factor, reputedly confusing in classification. The Gold Campine, on the other hand, carries all the corresponding recessive allelomorphs: gold, fast feathering, dark blue shanks, and dark brown eyes, as well as a number of additional contrasting characters of interest in other connections, such as those involved in down colors and patterns, ear-lobe and egg colors, hen-feathering in the male, etc.

The sex-linkages found were published in a preliminary note (MACARTHUR 1927); the values there reported have been confirmed in substance in the following years.¹ Meanwhile the number of known sex-linked genes has been increased and our knowledge of their localization in the sex chromosome has been extended by a number of other investigators (SEREBROVSKY and WASSINA 1927, WARREN 1928, HERTWIG and RITTERSHAUS 1929, RITTERSHAUS 1930, HERTWIG 1930). As might be expected from the large size of this chromosome (HANCE 1926), the number of sex-linked genes in the fowl is relatively large, seven at least having been determined up to the present, a greater number than is known in either of the autosomal linkage groups.

CHARACTERS AND FACTORS STUDIED

This report deals chiefly with the linkage relations between four pairs of sex-linked genes, of which the last, controlling light or dark iris color, is so studied for the first time:

¹ The carrying out of this project has been made practicable by the funds and stocks provided through the Department of Biology and the Poultry Department, and by facilities and direct help furnished by C. G. MACARTHUR at Bowmansville.

1. *Silver versus gold* (S, s)

These well known factors are easily distinguished in the ground color of the down of even the darkest chicks from the crosses listed below as 3, 4, 5, and 6. More difficulty and delay in classification in the first two crosses caused them to be early discontinued. Though silver is clearly dominant over gold, practically every Ss male bore numerous feathers partly gold, due probably to somatic segregation as described by SEREBROVSKY (1926).

2. *Slow versus fast feathering* ($K, k = Sl, sl$)

The rate of feathering is distinguishable with comparative certainty even in F_2 populations by the development attained by the wing quills at hatching and the length of the wing and tail feathers on the tenth day after hatching (WARREN 1925, 1928, 1930).

3. *Light versus dark dermal melanic pigmentation
in the shank* ($D, d = Y, y$)

The deep mesodermal pigment beneath the scales is slow developing and in young chicks is often quite masked at first by yellow lipochrome in the skin and for some time or permanently by the black epidermal pigment which occurs especially in the darkest downed chicks (crosses 1 and 2). At or about three months of age, as later rechecks show, the shank color becomes fixed and may be safely, and with few exceptions reliably, classified as either dark (slaty blue or green) or light (white, light blue, or yellow or light green)—(DUNN 1925). Since dark plumage colors blacken the shanks to a troublesome degree, crosses such as 5b and 6b producing pale or restricted black downs, are especially favorable.

4. *Light (yellow, orange to bay) versus dark (brownish
black) iris color*, (Br, br)

That the main genes controlling this contrast of eye colors are a sex-linked pair is concluded from their typical criss-cross inheritance, as in the reciprocal matings 5 and 6, and from their linkage relations. Such a conclusion has only been gradually won, after a period of confusion and change of views calling to mind the history of dark shank color inheritance.

The range and breed distribution of eye colors in fowls were described by DAVENPORT (1906), who observed that black eye tends to become associated with black plumage. Iris colors were classified histologically by BOND (1919) after the early plan devised for mammals, as: (1) simplex (*pearl*), with no anterior pigment and only a rather opaque stroma to obscure the posterior uveal color in hexagonal cells; (2) duplex, with one layer of anterior pigment, either (a) *yellow* or *red*, the round granules concentrating around connective tissue and in muscle fibres, or (b) *brown* or

black, the granules packed in a rich plexus of branching cells; and (3) the doubly pigmented triplex, as in Silky, where a *black* plexus overlies a deeper and separate yellow layer and the melanism is wide spread in corium and other mesodermal tissues. This order was considered in general as the order of ascending dominance or epistasis. In fact, however, it seems that but a few of the published crosses exhibit such autosomal dominance of the brown over the red or yellow eye.

DAVENPORT (1906) noted in F_1 hybrids from Black Minorca ♀ × Dark Brahma ♂ the imperfect dominance of yellow iris over brown. From matings of pearl-eyed Malay or yellow-eyed Buff Orpington hens with Black Orpington cocks BOND (1919) obtained chicks with black down and irides dark at first; but the cockerels became light-eyed at maturity by the gradual withdrawal or atrophy of the surface layer of branching cells containing the brown granules, while the pullets remained dark-eyed. He suggested that this change was sex-limited, but apparently did not make the corresponding reciprocal crosses to exclude the possibility of ordinary sex-linkage. PUNNETT (1923, pp. 157 and 58) found dark eye dominant in Sebright × Hamburg, but both dark eye and dark shank recessive and apparently sex-linked in the F_1 generations from reciprocal crosses of Brown Leghorn × Black Langshan; also sex-linked was melanism in the Silky × Brown Leghorn matings. Since the main object of this work is to collect, compare, and interpret observations, it is necessary to dissent from PUNNETT'S reference to Spangled Hamburgs and Campines as "dark-eyed and purple-faced" breeds; at least our stock of the former was orange-eyed, and neither breed had the purple in the face, comb and ear-lobe that is found in Silky and some Sebrights. In our crosses the sex-linked type of inheritance has been generally followed.

The chick iris color is evidently somehow influenced by epidermal plumage melanins, and the definitive color, either dark or light, becomes established only with advancing maturity. The presence or absence of the deep brown pigment in the adult iris is not then constantly associated with any particular color in the plumage, shanks, or skin, for in our segregating populations, as in pure breeds of fowls, either the dark or the light eye may be found with either of the skin and all the shank colors and with a great diversity of plumage colors and patterns. Dark-eyed F_2 birds, for instance, range in plumage color, either in the gold or the silver series, from black, through Campine marked, to the flecked, and to the nearly pure white of a very restricted Columbian pattern, and they may have shanks of any of the four main color groups. The breed correlation between black feathers and dark shanks and eyes is also broken in many exceptions, where black fowls have only one, or neither of the latter characters. Conversely, light plumaged F_2 birds with restricted black some-

times have one, the other, both, or neither of them. These crosses do not show what effects, if any, are exerted on iris colors by genes for the various recessive whites, barring, and a number of other colors and patterns. Since the pale birds from crosses 5b and 6b (p. 214) do not develop deep brown eyes, the fundamental color and certain melanin forming and extending factors are possibly prerequisites for the fully dark iris. In this material there was evidently no inhibitor of melanin common to shank and iris mesoderm, but the situations in Silkies and canaries and the known interrelation in mammals between eye and hair colors, hint that common distributing and interacting factors for these pigments in their different sites may be expected here.

5. *Li li*

Some observations of the relations of a fifth pair, *Li li*, controlling light or brown in the down have been gleaned from my notes since the literature on the sex-linked down color and pattern factors came to my notice.

CROSSES MADE

1. *Brown Leghorn* ♀, *D Br k s*, × *Silver Campine* ♂, *dd brbr kk SS*

The F₁ chicks were all silver and fast feathering, with black pigments so extended and intense as to conceal both parent down patterns, and make the shanks nearly black; the females were brown eyed, the males orange eyed. In the small F₂ population the females segregated for silver and gold; eye and shank color segregations could be followed in only a few favorable cases grown to maturity.

2. *Silver Campine* ♀, *d br k S*, × *R. I. Red* ♂, *DD BrBr KK ss*

The F₁ chicks were either uniform red-brown or campine patterned, the males silver and females gold, and both sexes slow feathering, with bluish-white shanks and slightly darkened yellow eye. In F₂ both sexes segregated for silver and gold, only the females for the remaining factors; silver here appears more frequently linked with dark shanks and dark eyes.

3. *Gold Campine* ♀, *d br k s*, × F₁ ♂, $\frac{D Br K s}{d Br k S}$, ex *R. I. Red* ♀ × *Silver Spangled Hamburg* ♂

The mating producing the male was first made to study the reported sex-linked spangling character (LEFEURE and RUCKER 1923), but this pattern behaved practically like an autosomal dominant.

4. *Columbian Plymouth Rock* ♀, *D Br K S*, × *Silver Campine* ♂, *dd brbr kk SS*

The F₁ chicks were all light to dark gray in down with light silver faces; the females being fast feathering, dark shanked and dark eyed, the males

slow feathering, light shanked and light eyed. The F_2 generation segregated for these three pairs.

5. *Columbian Plymouth Rock* ♀, *D Br K S*, × *Gold Campine* ♂, *dd brbr kk ss*

Both breeds carry black, which is non-extended in the Columbian pattern (*ReRe*), but the Gold Campine (unlike the Silver Campine) strains used differed among themselves in some melanin extension factors (whether *E^me^m*, or tine-atine—SEREBROVSKY 1926—or others), for in 1926, both in this cross and its reciprocal, 6 below, some pairings produced F_1 chicks of both sexes in two equal and very distinct classes:

a. Dark, slaty (extended), dove-gray to blackish-gray, chicks with light faces (gold in ♀ ♀, silver in ♂ ♂), but with no visible down striping.

b. Pale, non-slaty (restricted), all showing a distinct, but more or less modified Campine mottled or 4-striped pattern in the down. The females have less intensely brown eyes than in 5a.

c. New Gold Campine stocks obtained in 1928 from other sources, however, produced when crossed all dark chicks, 51 ♂ ♂ and 52 ♀ ♀, with sex distinctions as in 5a.

In crosses 5a, 5b, and 5c the F_1 females are all *d br k s*, the males $\frac{D Br K S}{d br k s}$, and the entire F_2 populations segregate for all four of the sex-linked character pairs. Reciprocal back-crosses and numerous F_2 *inter se* matings were made from 5c.

6. *Gold Campine* ♀, *d br k s*, × *Col. P. R.*, ♂

From this cross appeared both

a. Dark, slaty gray chicks with silver faces, and

b. Pale chicks with a Campine-like pattern of brown, black, and light stripes and flecks on the head, cheeks and back. All chicks, whether dark or pale, male or female, were slow feathering and finally developed orange eyes (with occasional faint brown dotting or rays) and light blue or white shanks. In the F_2 only females showed segregation and new crossover classes for the sex-linked factors.

CUTLER (1918) noted, but probably misinterpreted as somehow sex-linked, similar dark and pale classes in hybrids (all males) from Gold Campine ♀ × pheasant ♂.

DATA OBTAINED

A. *Segregation ratios for the different gene pairs*

From these crosses the ratios of the dominant and recessive allelomorphs were separately noted. In some matings as 1, 2, and 6, only females segre-

gated for some or all of the pairs. This fact, and the accumulating losses due to pests and natural deaths, account for the differences in totals. The sex, wherever doubtful, was ascertained by dissection, the sex ratio in F_2 being 269 ♂♂; 289 ♀♀. The other ratios totalled from all the crosses approximate the 1:1 expected, there having been classed: 334 silver: 359 gold; 309 slow feathering: 301 fast feathering; 186 light shanked: 201 dark; and as regards eye color, 191 reddish: 156 brown. No tendency was observed to a sex limitation in iris color or other genes.

*B. Linkage relations between the four pairs
of sex-linked genes*

Crossover results were taken from either the coupling or repulsion phase or both for all six groupings of the four pairs when they are taken two at a time. The bulk of the data is from the coupling phase in crosses 5 and 6. Tabulated separately in the notes for each phase in each of the crosses the ratios are here merely totalled (table 1). The percentages of crossing over were calculated without correction for differing viabilities of the classes.

TABLE 1
Showing the number and percentage of crossovers occurring between the series of sex-linked genes.

FACTOR PAIRS	SEGREGATION		TOTALS	CROSSOVER PERCENTAGES AND THEIR STANDARD ERRORS
	ORIGINAL COMBINATIONS	CROSSOVER COMBINATIONS		
<i>Ss</i> and <i>Kk</i>	520	69	589	11.7 ± 1.3
<i>Ss</i> and <i>Dd</i>	200	177	377	46.9 ± 2.6
<i>Ss</i> and <i>Br br</i>	210	164	374	43.8 ± 2.6
<i>Kk</i> and <i>Dd</i>	206	185	391	47.3 ± 2.5
<i>Kk</i> and <i>Br br</i>	171	157	328	41.8 ± 2.7
<i>Dd</i> and <i>Br br</i>	215	83	291	27.5 ± 2.6

The data indicate linkages of different intensities and significance. Shank colors show so high a percentage of crossing over with silver and gold (46.9 ± 2.6), and also with rate of feathering (47.3 ± 2.5), that assortment is practically free in both cases. Silver-gold and rate of feathering, however, are clearly and closely linked, with only 11.7 ± 1.3 percent of crossing over; this value is much smaller than the 19 percent found by SEREBROVSKY (1922), or the 14 percent of WARREN (1928), and more closely approaches the 10 percent suggested as most likely by HERTWIG and RITERSHAUS (1929).

Iris colors appear to show a definite though rather loose linkage with both silver-gold and rate of feathering, the crossover values being 43.8 ± 2.6 and 41.8 ± 2.7 percent respectively.

Between shank colors and iris colors another relatively close linkage is evident, for the crossovers are significantly low (27.5 ± 2.6 percent).

C. Linkage relations with other sex-linked genes

For reasons stated, barring was intentionally, though perhaps needlessly, avoided in this study; neither spangling nor ear-lobe color (WARREN 1928b) exhibited definite sex-linked behavior; and, though a relatively large number of F_2 chicks were found from crosses 5 and 6 which showed a head spot, and a 4-lined striping, phenotypically resembling those controlled by the *ko* and *st* genes, we have not been able to show in our material that either was sex-linked or associated with sex-linked genes.

The *Li li* factors which inhibit or produce brown in the down of non-black chicks (HERTWIG 1930, HERTWIG and RITTERSHAUS 1929) were not known to us when our notes were taken, but from the first it was clear that the F_2 campine-patterned and other markedly brown chicks were usually, but not invariably, gold and fast feathering. Of 52 such chicks from crosses 5a and 5c, 36 were gold and 16 silver, 35 fast feathering and 12 slow feathering, where equality would be expected, if sex linkage with *li* were not involved. In cross 6a, the 13 F_2 chicks which had been classified as campine-like were all (with one possible exception) females, as would be expected in dealing with the sex-linked *Li li* factors. Moreover, the corresponding class of light unstriped chicks, which are among those lacking brown in the down, show an equally marked excess of silver, slow feathering, light shanked and light eyed birds. A rough estimation of *li* linkages from these classes would seem justified since they result from autosomal segregation; the crossing over is about 31 percent between *S* and *Li*, 32 from *K* to *Li*, 16 from *D* to *Li*, and 23 from *Br* to *Li*. Naturally no great stress is to be laid on these figures in the quantitative sense.

D. Four-point tests

In crosses 5 and 6 the characters are suitably disposed in the parents and the F_2 populations reared large enough for a fairly reliable determination of the number of the single, double, and triple crossovers occurring in the F_1 male (table 3).

Among the 272 F_2 fowls, 96 (35.3 percent) represent original combinations, 120 (44.1 percent) single crossovers, 50 (18.4 percent) double crossovers, and 6 (2.2 percent) triple crossing over. The great frequency of double and triple crossovers is attributable to the great cytological length of the sex chromosome and the wide dispersal upon it of the loci studied. The triple crossovers are unexpectedly numerous; since all five *d Br k S* phenotype individuals were entered from a single small population, one of the first to be classified, it seems likely that the value given is too large.

In these tests the crossover percentages approximate those obtained from the whole body of data: *D-Br*, 29.9; *Br-K*, 47.7; *K-S*, 9.9; *Br-S*, 49.6; *D-K*, 44.4; and *D-S*, 46.3.

TABLE 2
Showing the frequencies of the different phenotypes segregating in the F_2 generation from

$$F_1 d br k s \text{ } \varnothing \times F_1 \frac{D Br K S}{d br k s} \text{ } \sigma^7, \text{ and among the female progeny from } F_1 D Br K S \text{ } \varnothing \times F_1 \sigma^7.$$

NON-CROSSOVERS	NUMBER	PERCENT
$D Br K S$	48	35.3
$d br k s$	48	
Single crossovers		
$d \mid Br K S$	22	11.1
$D \mid br k s$	8	
$d br \mid K S$	40	29.3
$D Br \mid k s$	40	
$d br k \mid S$	5	3.7
$D Br K \mid s$	5	
Double crossovers		
$d \mid Br \mid k s$	23	14.4
$D \mid br \mid K S$	16	
$d br \mid K \mid s$	3	1.8
$D Br \mid k \mid S$	2	
$d \mid Br K \mid s$	4	2.2
$D \mid br k \mid S$	2	
Triple crossovers		
$d \mid Br \mid k \mid S$	5	2.2
$D \mid br \mid K \mid s$	1	
Total	272	100.0

The numbers in the different classes unfortunately do not settle definitely the sequence of the genes, but silver appears to be more distant than rate of feathering from both D and Br loci, and Br would lie to the left of D .

SEX CHROMOSOME TOPOGRAPHY

Judging from the entire data here supplied, the loci of Ss and Kk are somewhat less than 12 units apart. From the average of all the determinations the Ss locus is separated by at least 44 units and that of Kk by at least 42 units from $Brbr$, and both Ss and Kk by still greater distances than these from Dd . Again, Dd and $Brbr$ are about 27.5 units distant. The observed $D-K$ and $Br-S$ crossover values agree well with calculated expectations. These and other recent data (HERTWIG 1930) seem to justify reversing the positions of K and S , suggested by SEREBROVSKY and WASSINA (1927) and WARREN (1928). Such meagre evidence as the material furnishes suggests that the locus of $Lili$ may be nearer to the center of the chromosome, rather than at the extreme right end (HERTWIG 1930). The

map localization of the four factor pairs might be represented as follows:

<i>D</i>	27.5	<i>Br</i>	42	<i>K</i>	12	<i>S</i>
<i>d</i>		<i>br</i>		<i>k</i>		<i>s</i>

The factors described above are apparently favorably distributed along the chromosome, the *Br br* genes helping to fill in the long empty central portion, and bridge over the wide gap between *D* near one end and *K* and *S* toward the other extreme. But it is still impossible to claim that this or any other present mapping of the sex chromosome is more than tentative, as compared with maps in *Drosophila*, maize, tomato, sweet pea, etc., though this is perhaps the best localized large group of linked genes that is offered in any vertebrate animal.

If we add barring, *B*, and the new genes for head spot, *ko*, and brown-in-down *li* (HERTWIG 1930, RITTERSHAUS 1930), we find uncertainties and inconsistencies also in the localization of these. Combining the data of all authors, and retaining the location of *ko* and *li* proposed by their discoverers, the following linear order and approximate spacings are suggested, merely as a working hypothesis:

<i>B</i>	<i>D</i>	23	<i>Ko</i>	<i>Br</i>	42	<i>K</i>	12	<i>S</i>	17	<i>Li</i>
<i>b</i>	<i>d</i>		<i>ko</i>	<i>br</i>		<i>k</i>		<i>s</i>		<i>li</i>

This provisional arrangement is based upon *one* interpretation of the crossover percentages contributed by the various workers in this field (HALDANE 1921, AGAR 1924, SEREBROVSKY and WASSINA 1927, WARREN 1928, HERTWIG and RITTERSHAUS 1929, HERTWIG 1930, RITTERSHAUS 1930). This data has been reviewed recently in the four last named papers, and further summary is unnecessary.

A critical examination and comparison of the findings shows that where several determinations of a value have been made, their agreement in details is generally good, and often excellent. Yet there are doubtful general points and not a few evidences of internal disharmony in the proposed arrangement as a whole. Such loose linkages have had to be used in the map construction that they provide no very accurate estimate of distances between genes or even of the actual linear order of the genes. Even the point test is no panacea in such a difficulty.

The precise linear relations of *B* and *D* are not sure, since, owing to the masking influence exerted by barring over shank color (WARREN 1928a), their positions and distance are necessarily found only indirectly through third genes. Further and new tests of the linkage of *B* and *D* with the not too distant head spot and iris color genes will doubtless greatly improve the known topography of the left half of the chromosome.

Crossover values between *ko* and *br* have never been taken, but their linkage is theoretically close. When suitable stocks have been found for

making this determination it will be interesting to see how well observation checks with theory in the central portion of the map.

The greatest quantitative discrepancies concern the location of the newer, less investigated genes, particularly *li*. The reported *B-Li* and *D-Li* crossover values are so low—40 and 31 percent respectively—as to appear decidedly anomalous and unlikely, if these genes lie at opposite ends of a chromosome over a hundred units long. *Li* may need to be relocated; in fact the map would fit the present data nearly as well if the *K S Li* section were inverted.

To ascertain the proper order of *K* and *S* in the right half of the chromosome, their linkages will have to be studied with genes that are closer than are *B* and *D*, and perhaps even closer than *Ko* and *Br*.

SUMMARY AND CONCLUSIONS

From Columbian Plymouth Rock × Gold Campine, and other interbreed crosses, the linkages were studied of the four pairs of sex-linked genes controlling silver or gold in the down and plumage (*S*, *s*), slow or rapid feathering (*K*, *k*), light or dark dermal shank color (*D*, *d*), and orange or brown iris color (*Br*, *br*), the last named pair being new in such studies.

The percentages of crossovers, with their standard errors, found were: *Ss-Kk*, 11.7 ± 1.3 , *Ss-Dd*, 46.9 ± 2.6 , *Ss-Br br*, 43.8 ± 2.6 , *Kk-Dd*, 47.3 ± 2.5 , *Kk-Br br*, 41.8 ± 2.7 , and *Dd-Br br*, 27.5 ± 2.6 .

These values, though not in full agreement with results of a large four-point test, indicate the most likely linear order and the approximate spacings of these genes to be:

Dd 27.5 *Br br* 42 *Kk* 12 *Ss*

A very provisional mapping of the sex chromosome, on the basis of all the published data and including the loci of barring, *B*, head streak, *ko*, and brown-in-down, *li*, genes, demonstrates a great number of uncertainties and inconsistencies in the proposed arrangement requiring correction by further investigation.

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