SEX-LINKAGE IN THE SILVER SPANGLED HAMBURG FOWL

by

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INTRODUCTION

In 1906 Punnett and Bateson discovered the phenomenon which they termed gametic coupling. It was found that two factors coming from the same parent segregate together. When the unit characters of animals and plants are more numerous than the chromosomes it is evident that more than one determiner, or factor must be carried in the same chromosome and that these must segregate together. The tendency of characters to remain together is termed "linkage". If other factors besides those for sex are borne in the chromosome, then they are sex-linked and segregate with the sex element as a unit.

It has long been known that color-blind persons are commonly males and that they transmit this quality not to their sons, but to their grandsons through their daughters. The daughters, although not color-blind themselves, transmit the defect to half their sons. The unaffected males never transmit the peculiarity and their progeny are free from this condition, unless it be introduced anew.

This phenomenon was often described but was not understood until the results of Mendelian analysis of heredity made this special mode of inheritance clear. Color-blindness is a recessive condition and is inherited in a typically sex-linked fashion.

TYPES OF SEX-LINKAGE

There are two types of sex-linked inheritance. In one,designated the Drosophila type,the male is heterozygous and the female homozygous for sex and sex-linked characters. In the other, the Abraxas type, the male is homozygous and the female heterozygous for sex and sex-linked characters.

The genetic evidence thus secured has placed in the Drosophila type the following organisms: Drosophila, man, cat, and the plants Lychnis and Byronia. The cytological evidence indicates that bugs, flies, beetles, grasshoppers, spiders, certain worms, amphibia andmammals also belong to the same type.

THE DROSOPHILA TYPE. The inheritance of white eye color in Drosophila will serve as an illustration of a typical case of this type. If a white-eyed male is bred to a red-eyed female, the F_1 sons and daughters have red eyes. If the F_1 generation is interbred, the F_2 offspring appear in the ratio of three reds to one white, but the white-eyed flies are all males.

To understand these peculiar results it is necessary to know the distribution of the sex-chromosome. In the female of Drosophila there are two sex-chromosomes (XX). After the reductional division there is one (X) sex-chromosome remaining in each egg. In the male there is one sex-chromosome (X) which has a mate termed the Y chromosome. The Y chromosome, when it is present, always remains in the male line. In some forms, however, the Y is not present and the X chromosome moves whole to one or the other pole of the spindle at the reductional division. In Drosophila there are two classes of spermatozoa: one class which contains the sex-chromosome and another class which does not, the latter carrying the Y when it is present. Owing to the reduction of the diploid group of chromosomes to the haploid group during maturation, each egg receives one X, while half of the male gametes contain and half lack the X chromosome. The sex of the resulting progeny will be determined by the kind of spermatozoon that fertilizes the egg. If the spermatazoon containing the X chromosome enters the egg,the resulting zygote will contain two sex-chromosomes (XX) and will consequently be a male. If the egg be fertilized by a spermatozoon containing the Y but not the X chromosome, the zygote will carry but one X chromosome and will be a male.

In the red-eyed female of the above cross each egg contains a sex-chromosome carrying the factor for red eyes. In the white-eyed male, half of the spermatozoa contain the sex-chromosome which carries the factor for white eyes, and half the Y chromosome which carries no white-eyed factor. When an egg,which contains the sex-chromosome, bearing the red-eyed factor is fertilized by a spermatozoon introducing the white-eyed factor, it will contain a red bearing sex-chromosome and a white bearing sex-chromosome. This will give rise to a red-eyed female, because the red dominates the white.

The egg that is fertilized by the non X bearing spermatozoon will produce a red-eyed male,because the single X chromosome introduces the factor for red eyes from the mother. At the maturation and reduction of the chromosomes in the germ cells of the F_1 female,two kinds of eggs are produced, half having the red-bearing and half the white-bearing sex-chromosome. Half of the male gametes contain the red-bearing X chromosome, while the other half contain the Y but lack the X chromosome. Random meeting of these different kinds of eggs and sperm will result in the 3:1 ratio of the ordinary Mendelian crosses in which dominant and recessive factors are concerned; but all the white-eyed progeny of the F_2 generation will be males. The F_2 generation males will have the red eyes, if the red-bearing sex-chromosome is transmitted to them by their mother, and white eyes, if they receive from her the white-bearing sex-chromosome. As all the female-producing spermatozoa will carry the factor for red eyes, all the F_2 generation females will have red eyes. Half of the F_2 females will be heterozygous and half homozygous for this factor.

Let X = sex-chromosome
" Y = the synaptic mate of the sex-chromosome.
" XX = female formula
" XY = male formula
" __ = sex-linked factor for red eyes

	Red-eyed Female		White-eyed Male	
	$\underline{X}$ $\underline{X}$		X Y	
Gametes	$\underline{X}$		X	Y
F_1	$\underline{X}$ X		$\underline{X}$ Y	
Gametes	$\underline{X}$	X	$\underline{X}$	Y
F_2	$\underline{X}$ $\underline{X}$	X $\underline{X}$	$\underline{X}$ Y	X Y

In the reciprocal cross very different results are obtained. When the white-eyed female is mated to a red-eyed male, the daughters will be red-eyed and the sons white-eyed. When these are interbred, white-eyed and red-eyed progeny appear in both sexes in the ratio 1:1.

The two sex-chromosomes in the mother carry the factor for white eyes. After ripening each egg contains one white-bearing X chromosome. Since the female-producing X chromosome of the red-eyed father carries the red factor, all the F_1 females will be red-eyed. As the single X chromosome of the F_1 males come from the white-eyed mother, it will carry only the factor for white eyes. Accordingly all the F_1 males will be white-eyed.

There are two classes of gametes in the F_1 females: one bearing the factor for white eyes and the other the factor for red eyes. Half of the male gametes contain the sex-chromosome bearing the white-eyed factor, and half have no sex-chromosome, and therefore, neither the red-eyed nor the white-eyed factor.

Reciprocal Cross.

	White-eyed Female		Red-eyed Male	
	X X		$\underline{X}$ Y	
Gametes	X		$\underline{X}$	Y
F_1	X $\underline{X}$		X Y	
Gametes	X	$\underline{X}$	X	Y
F_2	XX	$\underline{X}$X	XY	$\underline{X}$Y

Since there are two kinds of female gametes for the eye color, there will result two classes of males, red-eyed and white-eyed. An egg, bearing a factor for red eyes, fertilized by a female-producing spermatozoon bearing the white-eyed factor, will result in a red-eyed female. An egg, bearing a factor for white eyes, fertilized by a female-producing spermatozoon bearing the white-eyed factor will result in a white-eyed female. This produces half white-eyed and half red-eyed males; and half white-eyed and half red-eyed females.

In the different forms studied under the Drosophila type, there has always been a constant parallelism between the cytological evidence and the breeding results.

THE ABRAXAS TYPE. Genetic evidence places in this type several moths, butterflies, poultry, pigeons and canaries. Favorable cytological study has been found only in the case of a few moths. Because of the lack of knowledge of the chromosomes in this type, light has been thrown on the possible mechanism of sex-inheritance and sex-linkage only through the breeding results. Experimental breeding has shown conclusively that the male is homozygous, or double-dosed, as it were, for the sex factor, and therefore, it is assumed, must carry two sex-chromosomes; while the female is heterozygous, presumably having only one sex-chromosome. This is the exact reverse of what is true of forms belonging to the Drosophila type. Each male gamete must contain one chromosome bearing sex and sex-linked factors, while only half of the matured eggs of the female can have a sex-chromosome, which will also carry factors for sex-linked characters. The other half of the eggs lack the sex-chromosome, and, therefore, cannot transmit determiners for sex-linked characters.

If the two kinds of eggs, one set lacking and the other set containing the sex-chromosome, are equally numerous, and if the chances for fertilization are equal, then the union of two gametes, both carrying sex-chromosomes, determines a male. When only one sex-chromosome is present in the zygote, a female is produced. Thus, the fertilization of an egg that does not contain a sex-chromosome, by any male gamete, will result in a female. It is evident, then, that in the male progeny the factors for sex-linked characters come from both the male and the female lines; while the female progeny inherit such factors only from their sire. Thus, in a reciprocal cross the male will have the same characters, but the females will be different because they have different sires. The female always transmits the one sex-chromosome and its sex-linked factors to the male progeny.

A typical case of this kind has been described by Spillman and by Pearl and Surface in the inheritance of the barred pattern of the barred Plymouth Rock fowl.

Crossing the Barred Plymouth Rock females with Indian game males, the first generation results in heterozygous barred males and non-barred females. When these are inbred, both heterozygous barred and non-barred males, and barred and non-barred females are produced. The F_1 males are all barred because they inherit the single sex-chromosome bearing the barred factor from their barred mothers. The father transmits to his daughters one of his two sex-chromosomes, neither of which bears the factor for barring. Therefore, only non-barred F_1 females are produced. Since the F_1 male gametes are of two kinds, barred and non-barred, the result will be two classes of F_2 females of the same type as their sire. As the F_1 female gametes are all non-barred and the F_1 male gametes are half barred and half non-barred, the F_2 males will produce barred and non-barred progeny in the ratio 1:1.

When the reciprocal cross is made by mating barred males to non-barred females, the males of the F_1 generation will all be heterozygous for the barred factor. The females will also be barred, as they receive one of the sex-chromosomes carrying the barred factor from their sire. In the F_2 inbred generation both heterozygous and homozygous barred males and both barred and non-barred females are obtained. The females are of both kinds, because the father's gametes are of two kinds. His gametes contain sex-chromosomes, half of which bear the barred and half the non-barred factor. This explains the two possible types of females. Since the factor for barring in the F_1 females will always remain in the X chromosome, all the male producing eggs will carry the barred factor and consequently all the F_2 males will be half homozygous and half heterozygous for the barred factor.

Goodale ('09-'11) collected experimental evidence for sex-linked barring from crossing Barred Rocks with Buff Rocks and Barred Rocks with Brown Leghorns. The results of these matings are given in table 1.

Table 1

Inheritance of barring in barred x non-barred matings.*

		♂		♀	
1.		barred	x	non-barred	
	Gametes	(B (B		b	
	F_1	Bb		B	All birds are barred.

*B= barring factor dominant
b= non-barred, or absence of barring.

	♂		♀	
2.	non-barred	x	barred	
Gametes	(b (b		B.	
F_1	Bb		b	All ♂♂ barred; All ♀♀ non-barred

3.	F_1(barred ♂ x non-barred ♀)x F_1(barred ♂ x non-barred ♀)		
Gametes	(B (b	B	
F_2	(BB (Bb	B b	All ♂♂ barred; females 50% barred: 50% non-barred.

4.	F_1(non-barred ♂ x barred ♀)x F_1(barred ♀ x non-barred ♂)		
Gametes	(B (b	b	
	Bb bb	B b	50% of ♂♂ and 50% of ♀♀ non-barred; others barred

Pearl and Surface conclude in addition that "the general results indicate that (a) the barred pattern is inherited as a unit character independent of the pigment which fills the pattern, and that (b) more intense pigmentation is dominant over less intense with the final result, that (c) the actual somatic barring is less well defined in the barred hybrids than in their barred parents. Further, the ground color of the barring is different in the hybrids from what it is in their barred parents.

It is shown that there is no evidence of a blended inheritance of degrees of intensity of pigmentation."

In a series of experiments Punnett and Bateson analyzed the inheritance of the mesodomal pigmentation of the Silky Fowl. The unpigmented skin seems to contain an inhibitor (I) which the pigmented skin of the Silky fowl lacks. Table 2 gives the matings and the proportion of the various types to be expected in the results. The relation of the experimental results to the expectations was not always identical, probably because of disturbing physiological factors.

Table 2

		♂♂		♀♀	
1.		Brown Leghorn	x	Silky	
	Gametes	(I (I		i	
	F_1	Ii		I	In all hybrids melanogenesis is inhibited.
2.		Silky	x	Brown Leghorn	
	Gametes	(i (i		I	
	F_1	Ii		i	In all males melanogenesis partly inhibited; but in ♀♀ not.

	♂	♀	
3. F_1 Silky ♂ x Leghorn ♀) x F_1(Silky ♂ x Leghorn ♀)			
Gametes	(I (i	i	
F_2	(Ii (ii	I i	In both sexes approximately half have and half lack the melanogenetic inhibitor.
4. F_1(Leghorn ♂ x Silky ♀)x F_1(Leghorn ♂ x Silky ♀)			
Gametes	(I (i	I	
F_2	(II (Ii	I i	No fully pigmented male birds expected(though some found) as young:and ♀♀ half pigmented, half unpigmented.
5. F_1(Leghorn x Silky) x Brown Leghorn			
Gametes	(I (i	I	
Offspring	(II (Ii	I i	No fully pigmented ♂♂; half of the ♀♀ pigmented.
6. Brown Leghorn x F_1(Leghorn ♂ x Silky ♀)			
Gametes	(I (I	I	
Offspring	II	I	In all birds deep pigmentation is inhibited.
7. F_1(Leghorn x Silky) x F_1(Silky ♂ x Leghorn ♀)			
Gametes	(I (i	i	
Offspring	(Ii (ii	I i	In both sexes equal numbers of unhibited and inhibited pigmentation.

8.	Silky	x F_1(Leghorn ♂ x Silky ♀)	
Gametes	(i (i	I	
Offspring	Ii	i	In all ♂♂ pigmentation only partly inhibited; all ♀♀ deeply pigmented.
9.	Silky	x F_1(Silky ♂ x Leghorn ♀)	
Gametes	(i (i	i	
Offspring	ii	i	All offspring fully pigmented.

C.B.Davenport ('11) found that, in crossing the Brown Leghorn with the Dark Brahma, a sex-linked character appeared in the lacing of the wing bar and hackle. The Brown Leghorn has the hackle and saddle feathers laced with red, while in the Dark Brahma the red is replaced by white. The sons of the reciprocal crosses are nearly identical, being white laced with red wing bar. The white lacing is dominant, but the red wing bar is recessive. In the case of the daughters, when the father is white laced, the daughters are also; if the sire is red laced, the daughters have the same character. This peculiarity is due to the fact that the daughter inherits the lacing only from the father in a typical sex-linked fashion. The F_2 generation results are also in accordance with the assumption that the factor for lacing is borne in the sex-chromosome, the male having two sex-chromosomes while the female has only one.

From the fact that certain strains of poultry lay large numbers of eggs and others are comparatively unproductive, it would seem that egg production is inherited. Breeding from high producing hens apparently has not raised the average of the flock. The tendency has been to revert to the mean of the flock, and high producers have not given the looked-for increase in production.

The records show that hens divide themselves into the following groups with respect to their ability to produce eggs: (1) Those having a record of over thirty eggs during the winter months, Nov.1 to March 1; (2) those with a record of less than thirty eggs during this time; and (3) those showing no winter production.

In a series of experiments carried on at the Maine Experiment Station for a number of years, Pearl ('12) has obtained extensive data bearing upon the inheritance of egg production. For material he used Barred Plymouth Rocks and Cornish Indian Games. His conclusions are as follows:

"(1). There are three distinct and separately inherited factors upon which fecundity in the female fowl depends.

(2). The first of these factors (which may be called the anatomical) determines the presence of the ovary, the primary organ of the female sex. The letter F is used throughout to denote the presence of this factor.

(3). There are two physiological factors. The first of these (denoted by L_1) is the basic physiological factor, which when present alone in a zygote with F brings about a low degree of fecundity (winter record under thirty eggs). This factor is under no limitations in gametogenesis but may be carried in any gamete, regardless of what other factors may be also present.

(4). The second physiological factor (denoted by L_2) when present in a zygote together with F and L_1 leads to a high degree of fecundity (winter record over thirty eggs). When L_1 is absent, however, and L_2 is present, the zygote exhibits the same general degree of fecundity (under thirty) which it would if F_1 were present alone. These two independent factors L_1 and

L_2 must be present together to cause high fecundity, either of them alone, whether present in one or two "doses" causing the same degree of low fecundity.

(5). The second physiological factor L_2 behaves as a sex-limited)sex-correlated or sex-linked) character, in gametogenesis, according to the following rule: the factor L_2 is never borne in any gamete which also carried F. That is to say, all females which bear L_2 are heterozygous with reference to it. Any female may be either homozygous or heterozygous with respect to L_1. Any male may be either homozygous or heterozygous with respect to either L_1, L_2, or both."

Table 3

SHOWING THE OBSERVED AND EXPECTED DISTRIBUTIONS OF WINTER EGG PRODUCTION FOR ALL MATINGS TAKEN TOGETHER

Mating	Class	Winter Production of Daughters		
		Over 30	Under 30	Zero
All B.P.R.xB.P.R.	Observed	365½	259½	31
	Expected	381.45	257.25	17.30
All C.I.G.x C.I.G	Observed	2	23	15
	Expected	0	25	15
All F_1.	Observed	36	79	8
	Expected	26.5	88.75	9.75
All F_2 & back-crosses..	Observed	57.50	98.50	23
	Expected	68.60	95.00	15.40

Table 3 gives a summary of all the crosses and illustrates how well the hypothesis agrees with the facts. Considering the nature of the material and the type of work, the observations agree very closely with the expectation. Disturbing physiological factors would necessarily affect the observations to some extent and consequently there would be some divergence of the results from the expectations.

Goodale crossed the Brown Leghorn with the White Plymouth Rock and found that a complicated sex-linked inheritance occurs in regard to the color pattern. The White Rock carries the barred factor (B) but lacks the color factor (C). Letting L equal the determiner for Brown Leghorn coloration and l its absence; C the color factor (which is not sex-linked) and c its absence, the following table (4) shows a close agreement between expectation and results.

Table 4

	♂♂		♀♀	
1.	White Rock	x	Brown Leghorn	
Gametes	(Bc (Bc		LC -C	
F_1	BcLC		BCc	Both sexes barred; the males only splashed with Brown.

	♂		♀	
2.	Brown Leghorn	x	White Rock	
Gametes	(L (L		B	
F_1	BL		L	The males only barred; females either black with orange laced hackle, or approximately Brown Leghorn.

3.	White Rock	x F_1(White Rock ♂ x Brown Leghorn ♀)	
Gametes	(Bc (Bc	BC or Bc -c or -C	
Offspring	(BBcc (BBCc	Bcc BCc	Half ♂♂ white; half barred; ♀♀ half white, half barred.

The numbers of the progeny obtained were small; the results, however, indicated that the White Rock carries the barring as a sex-linked factor, but, owing to the absence of the color factor, they are white. When the color factor is introduced, the characteristic sex-linked inheritance of barring results.

Sturtevant ('11) also described a sex-linked inheritance of the black and red markings of the Brown Leghorn and the gray of the White Wyandotte. All the daughters inherited the brown from their Brown Leghorn father, while in the reciprocal cross, all the daughters were grey. In both crosses all the males were grey.

SEX-LINKED INHERITANCE OF SPANGLING

The results of this experiment show clearly that the spangled pattern of the Silver Spangled Hamburg is inherited as a sex-linked character belonging to the Abraxas type, although the inheritance may be modified by the presence of disturbing factors.

Factors for black, inherited independently of spangling, may obscure the spangled condition either on the entire body or on some definite portion of it. For example, black may affect the tail only or may cover the entire body, as is seen in the case of the F_1 males of the reciprocal crosses. The spangles themselves may be reduced in size by the spreading of the white back ground, until they become attenuated spots at the very tips of the feathers. In spite of these disturbances, the conclusion that there is a definite factor for spangling, which is sex-linked, seems entirely justified by the experimental results.

In the experiment described below the Silver Spangled Hamburg and the Brown Leghorn were used in the initial crosses. These breeds have different color markings and the latter shows a sex-dimorphism in both pattern and coloration. "The Brown Leghorn is nearly the color of the wild Gallus bankiva. The sexes are strongly dimorphic. The males have reddish yellow edging to the neck and back feathers, some red on the shoulders and wing coverts and a rather yellowish, brown lower web to the secondaries (wing-bay of the fanciers), the rest of the plumage being typically black. The female has the tail, primaries, upper web to secondaries, and stripe in neck-feathers black. Her breast is salmon yellow and the neck feathers are edged with yellow. The rest of the plumage is finely stippled or mossed with yellowish brown and black".

The Silver Spangled Hamburg has a characteristic black spangle at the tip of a white-based feather throughout the body in both sexes.

The experiments were undertaken for the purpose of determining, if possible, the mode of inheritance of this characteristic black spangling. The individuals are referred to below as spangled, or non-spangled. In former experiments in which the Brown Leghorn has been used, no evidence has been obtained that this breed transmits spangling, and, it is therefore, regarded as non-spangled.

MATINGS AND RESULTS

THE F_1 GENERATION. In the spring of 1913 were mated (Mating No.3) a Brown Leghorn cock No.205 (bred by the Poultry Department of the University of Missouri) and Silver Spangled Hamburg hens, Nos.3 and 72 (purchased of W.S.Binkley, Clay Center, Kansas). The reciprocal cross (Mating No.4) was made between a Silver Spangled Hamburg male, No. 40 and Brown Leghorn females Nos. 45 and 49 (photographs of chart of Mating Nos.3,4) Thirty-one chicks of Mating No.4 were raised to adults, and the type and distribution of color studied in each.

Mating Number 3

Brown Leghorn ♂ x S.S.Hamburg ♀

Expectation

	Male	Female
Zygotes	X X	$\underline{X}$ Y
Gametes	X X	$\underline{X}$ Y
Offspring	$\underline{X}$ X	X Y

The expectation for Mating No.3 would, therefore, be all heterozygous spangled males and all non-spangled females.

Mating Number 4

S.S.Hamburg ♂ x Brown Leghorn ♀

Expectation

Male	Female

Zygotes $\underline{X}\ \underline{X}$ x $X\ Y$

Gametes $\underline{X}$ $\underline{X}$ X Y

Offspring $\underline{X}\ X$ $\underline{X}\ Y$

The expectation for Mating Number 4 would, therefore, be heterozygous spangled males and spangled females, which, since the hens have only a single sex-chromosome, would also be heterozygous.

BREEDING RESULTS

The males derived from reciprocal crossing were practically alike, having spangled bodies with black tails, with the exception of four individuals (three in Mating Number 3 and one in mating No.4) which were entirely black. These black cocks later gave the same breeding results as their spangled brothers, and are evidently of the same genetic composition with respect to their ability to transmit spangling. The presence of multiple factors for black is probably responsible for the concealment of the spangled pattern of these birds. The daughters of the reciprocal crosses were strikingly different. Those from Mating No.3 were black with various degrees of brown stippling on the wings, while those of Mating No.4 had peculiar greyish feathers, showing crescentic pencilling with black and very distinct black spangles at the tip.

When the sires were spangled, the daughters were also spangled; if the father was non-spangled, his daughters had the same character. The daughters, then, inherited the spangling from the father's side only. The breeding results are in accord with the expectations given in the above tables of Matings Nos.3 and 4.

Assuming that a factor for spangling is borne in the sex-chromosomes, the results are readily explained by the mode of transmission of these chromosomes. Neither of the sex-chromosomes of the Brown Leghorn cock (No.205) in Mating No.3 carries the factor for spangling. The single sex-chromosome of the spangled female bears the spangled factor according to the hypothesis. The female will transmit the spangling to all of the sons, but to none of the daughters, while the male will transmit spangling to neither sons nor daughters, because he does not carry the factor for spangling in either of the sex-chromosomes. Thus, spangled males and non-spangled females are produced, the spangling acting as a dominant character in the heterozygous condition.

Contrasted with this, the silver spangled

Hamburg male (No.40) of the reciprocal cross,(Mating No.4) according to the hypothesis, should be homozygous for spangling as well as for sex. The Brown Leghorn hens, Nos. 45 and 49, being non-spangled, should not carry the factor for spangling in the sex-chromosome. From such a mating it is obvious that only spangled males and females would result, for the father transmits the spangling to his sons and daughters alike, while the mother, being non-spangled, will not affect the result.

The results obtained in the F_1 generation are, therefore, in accord with the expectation on the assumption that the inheritance of the spangled condition is sex-linked.

The occurrence of the black males in the F_1 generation would seem to introduce a complication, but their non-conformity is only apparent. To investigate the genetic constitution of these non-spangled black males, one of them, No.6791(B.S.♂ x S.S.H ♀) was mated to his non-spangled sisters, Nos. 3992 and 3998 (Mating No.16). If this cock were really non-spangled, as he appears to be, the expectation from this mating would be only non-spangled sons and non-spangled daughters, but such was not the result.

Mating No.16

F_1 Black cock 6791(Brown Leghorn ♂ x S.S.Hamburg ♀) x
F_1 hens 3992, 3998(Brown Leghorn ♂ x S.S.Hamburg ♀)

Expectation, if No.6791 does not carry the factor for spangling:

	Male	Female
Zygotes	X X	X Y
Gametes	X X	X Y
Offspring	X X	X Y

All of the resulting offspring would be non-spangled.

Expectation if he were heterozygous for spangling:

	Male	Female
Zygotes	X $\underline{X}$	X Y
Gametes	X $\underline{X}$	X Y
Offspring	X $\underline{X}$ XX	$\underline{X}$ Y XY

In this case the expectation would be spangled and non-spangled sons, and spangled and non-spangled daughters in equal numbers. This was observed to be the case in the breeding results.

The experimental data gave conclusive evidence that the black cock is really heterozygous for spangling and is identical with his spangled brothers in this respect. Although the lack of sufficient data prevents positive assertions, the black coloration is probably the result of a cumulative effect of multiple factors for the black, introduced by the Brown Leghorn, which masks the spangled pattern and prevents its appearance.

THE F_2 GENERATION. In the spring of 1914 the spangled hybrid cock, No.3983, from the same mating (No.3) as No.6791 (black) was mated to his non-spangled hybrid sisters, Nos. 3991 and 3995 (Mating 17).

Mating No.17

Spangled F_1 Male x Non-Spangled F_1 Female

3983 ♂ (Brown Leghorn ♂ x S.S.Hamburg ♀) x 3991(Brown Leghorn ♂ x S.S.Hamburg ♀)

Expectation

	Male		Female	
Zygotes	$\underline{X}$ X		X Y	
Gametes	$\underline{X}$	X	X	Y
Offspring	$\underline{X}$X	XX	$\underline{X}$Y	XY

The expectation in this case would be spangled and non-spangled sons and daughters in equal numbers. The actual results were in conformity with the theoretical expectation and both types of males and females were obtained. This result was the same as in Mating No. 16, and the experimental evidence in both cases agrees with the expectation.

The hybrids of the reciprocal cross (No. 4) were mated in Mating No. 14.

Mating No.14

Spangled F_1 Males x Spangled F_1 Females.

1153 ♂ (S.S.Hamburg ♂ x Brown Leghorn ♀) x 1160 ♀ ,1162 ♀ , 1165 ♀ (S.S.Hamburg ♂ x Brown Leghorn ♀)

Expectation

	Male		Female	
Zygotes	$\underline{X}$ X		$\underline{X}$ Y	
Gametes	$\underline{X}$	X	$\underline{X}$	Y
Offspring	$\underline{XX}$	$\underline{X}X$	$\underline{X}Y$	XY

As seen above the male is heterozygous for spangling; consequently two types of females are produced; spangled and non-spangled. The mother is spangled and transmits the spangled factor to her male progeny.The son is heterozygous for the spangling factor.It is obvious then, that the union of such gametes should result in heterozygous and homozygous spangled males and spangled and non-spangled females. The breeding results showed this to be the case, with the exception of the occurrence of two black males which are similar to the black males of Matings Nos. 3 and 4.

In the spring of 1915 several crosses were made to further test the mode of inheritance of spangling.

An F_1 spangled male No. 1153, from Mating No. 4, also used in Mating 14 was crossed with a Brown Leghorn hen (Mating 27).

Mating No. 27

F_1 Spangled Male x Brown Leghorn Female

1153 ♂ (S.S. Hamburg ♂ x Brown Leghorn ♀) x Brown Leghorn ♀ .

Expectation

	Male			Female	
Zygotes	$\underline{X}$ X		x	X Y	
Gametes	$\underline{X}$	X		X	Y
Offspring	$\underline{X}$X	XX		$\underline{X}$Y	XY

The expectation for this cross is heterozygous spangled and non-spangled males, and spangled and non-spangled females. The mating yielded six spangled and six non-spangled males and two spangled and four non-spangled females. The assumption that the hybrid cock, No.1153,is heterozygous for spangling is justified by these results.

An F_1 spangled male No.3987 was bred to Silver Spangled Hamburg females (Mating 15).

Mating No.15

F_1 Spangled Male x S.S.Hamburg Female

3987 ♂ (B.Leghorn ♂ x S.S.Hamburg ♀) x S.S.Hamburg ♀ .

Expectation

	Male		Female	
Zygotes	$\underline{X}\,X$		$\underline{X}\,Y$	
Gametes	$\underline{X}$	X	$\underline{X}$	Y
Offspring	$\underline{X}\underline{X}$	$X\underline{X}$	$\underline{X}Y$	XY

This mating should yield only spangled males, half homozygous and half heterozygous, and spangled and non-spangled females, which would be the same as the results obtained from Mating 14. In the breeding results the daughters were in accordance with the expectation. In addition to spangled males, two black males were obtained, but these, like the black cocks of the F_1, are probably due to a cumulative effect of multiple factors for black pigmentation.

In Matings Nos. 13 and 28, made in 1914, the Silver Spangled Hamburg (male No.40), used in Mating 4, was crossed with non-spangled F_1 females (Nos.3992 and 3995) and spangled F_1 females (Nos.1160, 1161 and 1162) respectively.

Mating No.13

Silver Spangled Hamburg Male x F_1 Non-Spangled Females 40(S.S.Hamburg)♂X 3992 ♀, 3995 ♀, (Br.Leghorn ♂ x S.S. Hamburg ♀).

Expectation

	Male	Female
Zygotes	$\underline{X}$ $\underline{X}$	X Y
Gametes	$\underline{X}$ $\underline{X}$	X Y
Offspring	$X\underline{X}$	$\underline{X}$ Y

The results of this mating should be the same as in the case of Mating No.4, in which the S.S.Hamburg cock was bred to a Brown Leghorn hen. The male is homozygous for spangling, and hence all the daughters should receive the spangled factor from their father. The sons should be heterozygous for thespangled factor, as they inherit spangling from their father but not from their mother. All the progeny should, therefore, show the spangled pattern. Ten spangled males and ten spangled females were obtained. Two black males and three black females also appeared in the progeny. None of these black birds has been tested, but it is assumed that their spangling is masked by black.

Mating No.28

Silver Spangled Hamburg Male x F_1 Spangled Female.

40 ♂ S.S.Hamburg x 1160 ♀ ,1161 ♀ ,1162 ♀ (S.S.Hamburg ♂ x Brown Leghorn ♀).

Expectation

	Male	Female
Zygotes	$\underline{X}\ \underline{X}$	$\underline{X}\ Y$
Gametes	$\underline{X}$ $\underline{X}$	$\underline{X}$ Y
Offspring	$\underline{X}\ \underline{X}$	$\underline{X}\ Y$

The expectation is only spangled progeny, and such is the case in the experimental results; but here again the effects of masking black pigmentation are evident. Instead of having clearly defined spangles, the daughters are very much like their obscurely spangled mothers. The sons are well spangled on the body, but the black partially covers the spangles in the tail, causing the males to have the appearance of the F_1 hybrid spangled males.

Mating No.29

Brown Leghorn Male x Non-spangled F_1 Female

Brown Leghorn ♂ x 3993 ♀ ,3994 ♀ ,(Brown Leghorn ♂ x S.S.Hamburg ♀).

Expectation

	Male	Female
Zygote	X X	X Y
Gametes	X X	X Y
Offspring	X X	X Y

This mating should yield only non-spangled progeny, and the expectation was realized, for all the sons and daughters were non-spangled. These appeared in the ratio of 14:15.

In Mating No.30, an F_2 spangled cock(No.6914,) and his spangled sister (No.6908), from Mating No.14 were crossed. Since this cock may be either homozygous or heterozygous for spangling, the results of the mating cannot be predicted. If he were homozygous for spangling, mating him to a spangled hen would obviously yield only spangled offspring; but if he were heterozygous, when mated to a spangled hen, the expected progeny would be spangled males, and spangled and non-spangled females, the males being heterozygous and homozygous for the spangling factor. In the experimental results three spangled males and four spangled females were obtained. Unfortunately the space did not permit the testing of all the resulting males of this cross to ascertain whether their condition for spangling was homozygous or heterozygous. All the progeny were spangled, but they were so few in number (only seven) as to leave a possibility for the occurrence of the non-spangled females, if a larger number of offspring had been produced.

In Mating No.31 a heterozygous spangled male (No.7005), was mated to a non-spangled sister (No.7007) from Mating No.17. The expectation would be both kinds of males and both kinds of females. The non-spangled males and spangled females were lacking. As only four individuals were obtained from this cross, no definite conclusions could be drawn from it.

RESULTS OF ALL THE MATINGS

Expectation	Mating	Non-Spangled		Spangled		Total Progeny
		Male	Female	Male	Female	
0:2:2:0	3	3(Blk)	9	19	0	31
0:0:2:2	4	1(Blk)	0	10	15	26
0:0:2:2	13	2	3	10	10	25

RESULTS OF ALL THE MATINGS(cont'd)

Expectation	Mating	Non-Spangled		Spangled		Total Progeny
		Male	Female	Male	Female	
0:1:2:1	14	2	8	10	8	28
0:1:2:1	15	2	5	1	3	11
1:1:[illegible]:1	16	4	5	2	2	13
1:1:1:1	17	2	5	4	1	12
1:1:1:1	27	6	4	6	2	18
0:0:2:2	28	0	0	2	5	7
2:2:0:0	29	14	15	0	0	29
0:0:2:2 ?	30	0	0	3	4	7
1:1:1:1	31	0	2	1	1	4

In the above results only feathers tipped with black spangles were regarded as the criterion of the inheritance of spangling. Spangling is genetically distinct from mottling, and in recording results the latter was considered as a non-spangled condition. All degrees of the spangling were observed from feathers terminating in a small black spot, to feathers which were black, except for a small white streak at the base. Since all the males of the F_1 and some of the males in the F_2 generation had black tails, it would seem that the Brown Leghorn introduces a factor which causes a spreading of black throughout the feathers of the tail. Other F_2 males approached very closely the original spangled pattern of the Hamburg. Birds were observed having both buff and white based feathers terminating in black tips, while others had plumage of black and buff base with the buff and white tips. Davenport states that "Of the mottled condition all degrees are found, from white splashed with black to black with white spots; also blue is very common in offspring of two mottled birds. The relation of these patterns is very complex, and much time would be required for their complete analysis; but it seems certain that there is a spangling or mottling factor, but that, as in canaries, guinea pigs, and rats, the precise pattern is not inherited. There are, to be sure, in poultry, so called races of spangled birds with well defined patterns, such as Spangled Polish, Spangled Hamburgs, and so forth, but it is the experience of breeders that they do not reproduce their patterns very closely."

Here Davenport apparently regards spangling and mottling as one and the same condition, or as associated conditions, but from the above data there seems to be a very distinct difference. The spangling condition is inherited in a sex-linked fashion, while the mottled condition seems to be very complex and the precise pattern not inherited.

CONCLUSIONS

(1). The above results are in accordance with the hypothesis that in poultry the male is homozygous for sex, and the female heterozygous; that the factors for certain characters are linked with the factors for sex.

(2). Spangling in the Silver Spangled Hamburg follows the sex-linked mode of inheritance.

(3). Spangling is inherited as a unit character independently of characters that are concerned with different degrees of pigmentation.

(4). Spangling is a unit character which segregates independently, and it may appear on the buff background inherited from the Brown Leghorn as well as on the white background of the Hamburg, as may be seen in different individuals of the F_2 generation. This would indicate the independent segregation of spangling as a definite unit.

(5). The factor for spangling is independent of a factor or factors for mottling which seems to have a complicated form of inheritance.

(6). The black cocks which transmit spangling, although adequate experimental data are lacking, would seem to be best explained by assuming the presence of multiple factors for black which may have a cumulative effect and conceal the spangled pattern.

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Acknowledgment is given herewith to Dr. George Lefevre, Chairman of the Zoology Department, for the assignment of the problems, and helpful suggestions and assistance during the progress of the work.

MATING NO.3

PARENTS

Brown Leghorn ♂

S.S. Hamburg ♀

MATING NO. 3 CONTINUED

OFFSPRING

-3981-

-6791-

-3992-

Male	Female
XX	XY
XX	XY

MATING NO. 4

PARENTS

S.S. Hamburg ♂

Brown Leghorn ♀

MATING NO.4 CONTINUED.

OFFSPRING

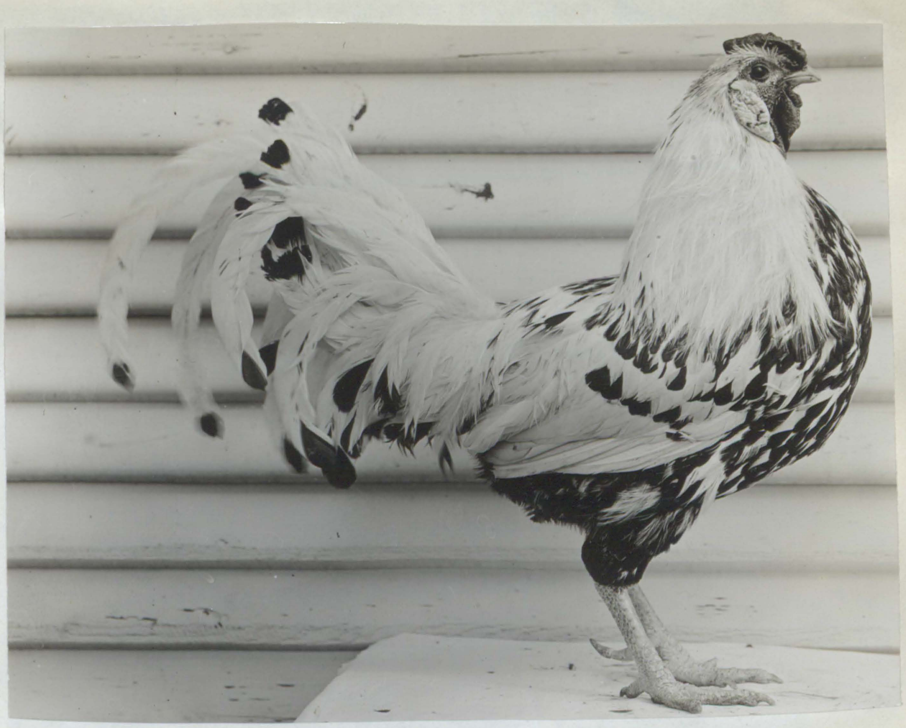
1153

1160

Male	Female
X X	X Y
X X	X Y

MATING NO.13

PARENTS



S.S. Hamburg ♂

-3992-♀-

Male	Female
X X	X Y
X X	X Y

MATING NO.13 CONTINUED

OFFSPRING

6865♂

6862♀

MATING NO.14
PARENTS

1153♂

1160♀

Male
-X X-

-X X-X X-

Female
-X Y-

-X Y-X Y-

MATING NO.14 CONTINUED

OFFSPRING

6913 ♂

6903 ♀.

6908 ♀.

MATING NO.15

PARENTS

3981♂

S.S.Hamburg.♀

Male	Female
X X	X Y
-X X-X X-	-X Y-X Y-

MATING NO.15 CONTINUED
OFFSPRING

6943 ♂

6953 ♀

6956 ♀

MATING NO.16
PARENTS

6791 ♂

3992 ♀

Male	Female
X X	X Y
X X X X	X Y X Y

MATING NO.16 CONTINUED.
OFFSPRING

6658(6656)♂

6659♂

MATING NO.16 CONTINUED
OFFSPRING

6953 ♀

6651 ♀

MATING NO.17
PARENTS

3981♂(3983)

3992♀

Male	Female
X X	X Y
X X X X	X Y X Y

MATING NO.17 CONTINUED

OFFSPRING

7005 ♂

6658(7003) ♂

MATING NO. 17, CONTINUED

OFFSPRING

6862 (7009) ♀

7007 ♀

MATING NO.27
PARENTS

1153 ♂

B. Leghorn ♀

Male	Female
X X	X Y
X X X X	X Y X Y

MATING NO.27 CONTINUED

OFFSPRING

6946♂

6921♂

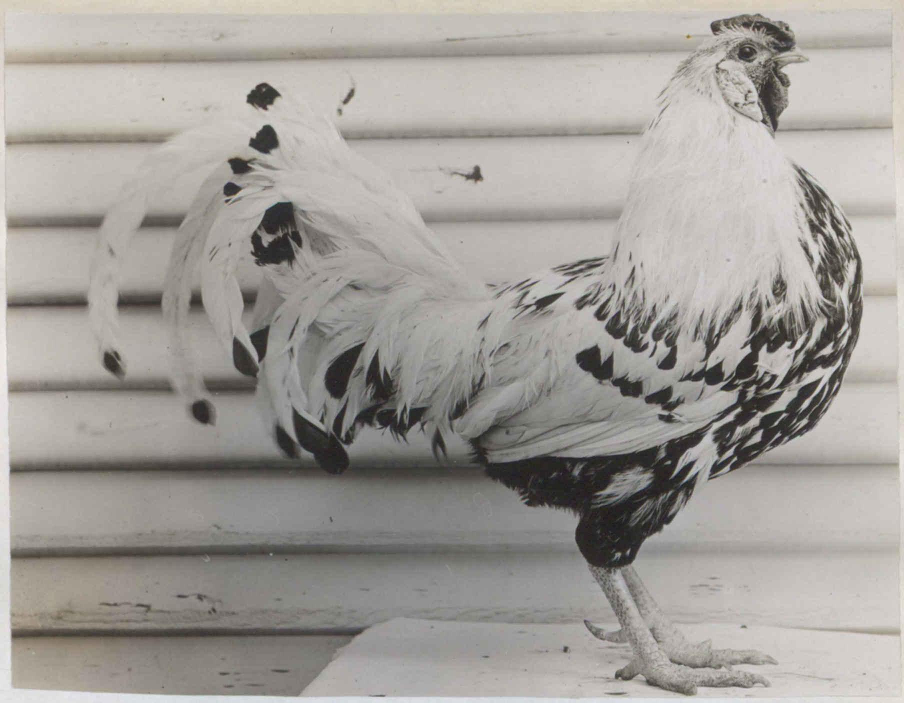
MATING NO.27 CONTINUED
OFFSPRING

6882 ♀

6947 ♀

MATING NO.28

PARENTS



S.S. Hamburg ♂

1160 ♀

Male	Female
X X	XY
X X	X Y

MATING NO.28 CONTINUED

OFFSPRING

6940 ♂

6942 ♀

MATING NO.29

PARENTS

B-Leghorn ♂

3992 ♀

MALE	FEMALE
X X	X Y
X X	X Y

MATING NO.29 CONTINUED

OFFSPRING

6927♂

6925♀

MATING NO.31

PARENTS

7005 ♂

7007 ♀

Male		Female	
X X		X Y	
XX	(X X	X Y)	X Y

Absent

Only five birds obtained from this cross.

MATING NO.31 CONTINUED
OFFSPRING

6938 ♀

6918 ♂

UNIVERSITY OF MISSOURI
COLUMBIA

ZOOLOGICAL LABORATORY

The dissertation of Mr. E. H. Rucker, entitled "Sex-linkage in the Silver Spangled Hamburg Fowl", is hereby approved and recommended for acceptance in partial fulfillment of the requirements for the Degree of Master of Arts

George Lefevre

May 16, 1916

UNIVERSITY OF MISSOURI
COLUMBIA

DEPARTMENT OF PHYSIOLOGY

May 27, 1916.

Dean Walter Miller,
Graduate School,
University.

Dear Sir:-

I wish to approve and recommend the thesis of Mr. E. H. Rucker as partial fulfillment of the requirements for the Master's degree. I note the following minor criticisms, bearing upon the historical introduction:- Historically and logically the work of the chromosomes has not served to prove "linkage", but rather vice versa. Also, although Guyer's contention that the cock possesses the odd chromosome seems to have been an error, it can hardly be ignored completely. It might also seem worth while to refer to the attempt by L. J. Cole, published some time ago in "Science", to harmonize these contrary findings.

In reporting the results and conclusions it may well be emphasized that sex-linked inheritance is shown with greater conclusiveness and completeness in these experiments than in any that are as yet reported in the literature. In bringing this out, I would suggest letting #2 of the conclusions become #1, with the present #1 coming after.

For my own aid in studying the results I found it necessary to add a column to the last tabulation of results. I would recommend that the table be made to include some such column as my pencilings have provided.

Very truly yours,

AG/O.

Addison Gulick