PLUMAGE AND EYE COLOR INHERITANCE IN THE SINGLE COMB RHODE ISLAND RED FOWL [1]

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STANDARD COLOR OF BREED

An examination of a flock of Rhode Island Red fowls shows the color of the plumage and eyes to be highly variable. In the average flock there are birds varying from a light shade (approaching buff) to a deep mahogany or bay color. The eyes also show a wide variation in the amount of red pigment in the iris. These variations exist in spite of the fact that the breed has been selected for years for a deep red color of both plumage and iris. The wide range of intensity of pigmentation found in this breed would seem to suggest that the ideal standard color is rather complex in the nature of its inheritance.

The American Standard of Perfection [2] gives the description of the ideal bird of the Rhode Island Red breed as specified by the American Poultry Association. This standard requires that the Rhode Island Red be of a deep reddish bay color throughout the plumage of both sexes. It is desired that all sections of the plumage be as uniform in color as possible. The under fluff of the feathers should also be of the same color as the surface.

Tipping of black is permitted in the neck feathers of females. Black color is also desired in the primary and secondary flight feathers of both sexes. The upper web of the primary feathers should be red and the lower web largely black. In the secondaries the color is reversed, the lower web being red and the upper one largely black. The main tail feathers of both male and female are black. The sickle and covert feathers are also black or greenish black in the males. The occurrence of white in any section of the plumage and of black, except where specified, constitutes a defect in color.

Very little has been published on the inheritance of the color qualities of the Rhode Island Red. Bittenbender [3] recommended that both male and female be the same color, and he further mentioned the necessity of having a bar of black pigment in the back feathers of only one parent to assure rich, red plumage color in the offspring.

Dunn [4] suggested that the Rhode Island Red carries the recessive gene e^m which restricts melanic pigment to the neck, wings, and tail. The standard established for this breed has caused the melanic pigment to be reduced to a minimum in regions, except the flight and tail feathers.

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[2] AMERICAN POULTRY ASSOCIATION. THE AMERICAN STANDARD OF PERFECTION . . . 1930 ed., 487 p., illus. n.p. 1930.

[3] BITTENBENDER, H. A. BREEDING RHODE ISLAND REDS FOR STANDARD TYPE AND EGG PRODUCTION. Iowa Agr. Expt. Sta. Bull. 202, pp. [11]–24, illus. 1922.

[4] DUNN, L. C. A GENE FOR THE EXTENSION OF BLACK PIGMENT IN DOMESTIC FOWLS. Amer. Nat. 56: 464–466. 1922.

Hays [5] in his proposed theory on the inheritance of color in the Rhode Island Red, suggested that three genes are responsible for the plumage pattern. The autosomal gene B for reddish-brown pigment, in combination with either a sex-linked gene L for color pattern and gold color or an autosomal gene E for the extension of melanic pigment, is responsible for the color phenotypes found in this breed. Hays did not attempt to account for the minor fluctuations which he suggests are probably due to the action of modifying factors.

The purpose of this study was to analyze, insofar as the available data will permit, the color inheritance in the Single Comb Rhode Island Red. The data upon which the analysis was made were taken from the Kansas Agricultural Experiment Station flock of this breed. The matings involved were made for the study of other characteristics in the fowl, but along with other records detailed color descriptions were also recorded for each individual. It was originally planned that this study would be preliminary to later ones where matings would be made for the specific purpose of the analysis of color inheritance. It now seems necessary to terminate the work on this project with the present paper.

MATERIALS AND METHODS

The stock used in this study had been handled and bred for some time as a production flock of Single Comb Rhode Island Reds, and an effort had been made to maintain fairly good standard qualities. Although there was considerable variation among individuals in this flock, the average color had been kept a good dark red.

In order to maintain uniformity and accuracy in classification of eye and plumage color, all descriptions were based on a set of color standards for each region considered.

The standards for feather color were the result of selection, after an examination of a large number of birds, of five gradations in color as being representative of the range of feather colors found in this breed. These feather standards served for classifying both surface and under color. The standard was made by mounting on a white cardboard samples of plucked feathers. Grade 1 was the lightest shade of color while the successive grades indicated increasing intensity of color. The standard colors of plumage and the standard for eye color were those used in a previous experiment by the senior writer.[6]

The descriptions of primary and secondary wing feathers follow a grading system based on the amount of black pigment found on the surface of the feathers of this region. The second full-length primary and the second secondary flight feathers were used for recording the amount of black. The numbers 1 to 6 are used to designate increasing amounts of black. Grade 6 occurred so infrequently that it was included in grade 5 in the summaries, thus only five grades were required in the tables. The range of variations found is shown in figure 1.

The eye color grades were based on the amount of red pigment in the iris. The iris color of each bird was compared with a color chart

[5] HAYS, F. A. INHERITANCE OF PLUMAGE COLOR IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL. Genetics 11: [355]-371. 1926.

[6] WARREN, D.C. THE INHERITANCE OF RHODE ISLAND RED CHICK DOWN-COLOR VARIATIONS AND THEIR RELATION TO COLOR VARIATIONS IN ADULT PLUMAGE. Jour. Agr. Research 39: 781-794, illus. 1929.

painted from representative specimens of grades of pigmentation. The grades ranged from an iris with practically no red to one showing a deep reddish bay color.

All descriptive observations were made at maturity (6 months of age), and the birds were graded according to the color standards for the respective regions. In order to secure uniformity in grading, all descriptions were made under natural lighting conditions and by the same person. In the description of the plumage color, the back, hackle, and breast were graded separately. In the study of under color, only the shade of red was considered.

Rather than preserve whole skins from so large a number of birds, feather samples from different regions of the plumage were preserved on cards as previously described by Warren.[7] Complete records were kept on all birds available for the breeding seasons 1927 to 1930, inclusive, totaling over 3,000 individuals.

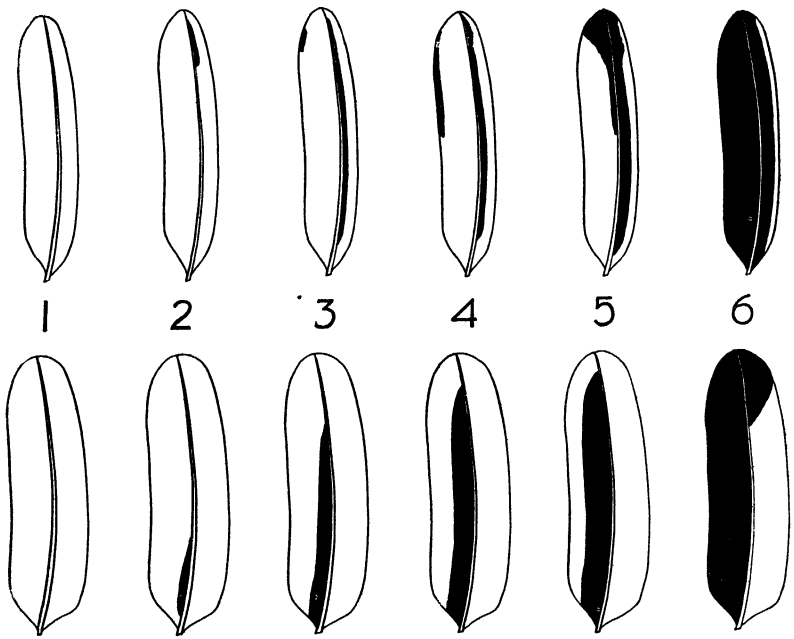

FIGURE 1.—Grade-number standards for variations in the amount of black pigment in the primary (upper series) and secondary (lower series) wing feathers of adult Rhode Island Red chickens.

RESULTS

In the study of color inheritance in various regions of the plumage the results were summarized on the basis of parental color combinations. The color grades of the offspring from the various paternal and maternal grades are shown in table 1. This made it possible to compare the results of mating the lightest colored female with the lightest colored male and darkest color with darkest color as well as reciprocal matings between color extremes. Because of the fact that birds in the extreme grades occurred infrequently and were mated

[7] WARREN, D. C. See footnote 6.

still less frequently, it was not possible to present the results of all color combinations. The various combinations of color grades were presented in the following tables insofar as they were available:

TABLE 1.—*Mean results from all available combinations of parental plumage and eye color grades*

BACK PLUMAGE

Sires' color grade (plumage)	Mean grade for daughters when the dams' color grade was—					Mean	Mean grade for sons when the dams' color grade was—					Mean
	1	2	3	4	5		1	2	3	4	5	
5	------	2.98	3.19	3.35	------	3.22	------	4.44	4.33	4.43	------	4.38
4	[a]2.75	2.71	2.99	3.10	3.61	3.07	[a]3.87	3.88	4.17	4.05	4.11	4.07
3	------	------	2.89	2.97	------	2.94	------	------	[a]4.05	4.15	------	4.12

BREAST PLUMAGE

5	------	[a]2.44	[a]2.44	2.75	------	2.66	------	3.38	[a]3.91	3.58	------	3.65
4	2.08	2.27	2.52	2.95	3.41	2.61	2.77	3.23	3.42	3.55	3.46	3.37
3	------	2.22	2.43	2.41	------	2.33	------	2.97	3.17	3.34	------	3.15
2	[a]1.18	2.17	2.07	2.45	------	2.14	[a]2.50	2.55	2.90	2.91	------	2.79

HACKLE PLUMAGE

5	------	[a]3.22	3.60	3.68	------	3.59	------	[a]3.88	3.96	[a]4.17	------	4.00
4	------	[a]2.89	3.31	3.32	[a]3.93	3.32	------	[a]3.29	3.77	3.82	[a]4.22	3.79
3	------	3.19	3.18	3.37	3.46	3.27	------	3.38	3.60	3.66	3.47	3.59
2	------	2.88	3.13	3.26	------	3.14	------	3.35	3.26	3.56	------	3.41

UNDER PLUMAGE

5	------	[a]2.42	2.33	[a]2.64	------	2.45	------	[a]3.09	[a]2.89	[a]2.60	------	2.91
4	[a]2.39	2.48	2.46	2.81	3.09	2.69	2.46	2.71	2.76	2.77	2.98	2.76
3	------	2.49	2.69	2.72	------	2.61	------	2.85	3.10	2.96	------	2.96
2	[a]2.59	2.30	2.54	2.61	------	2.50	[a]2.75	2.72	2.64	2.81	------	2.74

BLACK IN PRIMARIES

5	[a]2.73	2.68	2.93	3.21	------	2.84	[a]3.33	3.42	4.06	4.26	------	3.68
4	2.39	2.49	2.83	[a]2.90	------	2.63	[a]3.33	3.42	4.02	[a]3.72	------	3.61
3	[a]2.05	2.54	2.66	[a]2.88	------	2.60	[a]3.00	3.20	3.39	[a]4.00	------	3.35
2	[a]1.82	1.93	2.14	[a]2.83	------	2.04	[a]2.40	2.54	2.92	3.78	------	2.75

BLACK IN SECONDARIES

5	3.14	3.11	3.33	3.52	[a]3.90	3.35	[a]3.95	4.06	4.09	4.32	[a]4.19	4.13
4	2.30	2.82	2.92	3.18	3.31	2.87	3.23	3.50	3.87	4.33	[a]4.15	3.81
3	[a]2.39	2.18	2.16	[a]2.46	------	2.27	2.62	3.49	3.35	[a]3.50	------	3.22
2	1.91	2.22	2.52	[a]2.91	[a]2.63	2.39	[a]2.53	[a]2.86	3.38	[a]3.67	[a]3.91	3.20
1	1.66	[a]1.57	[a]2.31	------	------	1.87	[a]1.92	[a]2.21	[a]2.73	------	------	2.22

EYE COLOR

6	------	------	[a]9.39	9.23	------	9.27	------	------	[a]8.83	8.74	------	8.75
5	[a]9.40	9.29	9.88	9.56	9.63	9.55	[a]10.00	9.52	9.85	9.82	10.00	9.80
4	[a]8.69	9.22	9.38	9.52	9.36	9.39	[a]9.33	9.55	9.44	9.64	9.69	9.47
3	[a]8.75	9.27	9.09	9.46	[a]9.30	9.24	[a]8.54	9.41	9.07	9.24	[a]9.27	9.17

[a] These means are for classes of less than 30 individuals.

The inheritance of the shade of red color was studied in four regions of the plumage: Back (mid-dorsal region); breast; hackle, which is the collar of long pointed feathers covering the base of the neck; and the under surface, which includes the fluff at the base of the feather. The under color was that of the mid-dorsal region. There is frequently considerable contrast in the shade of red in these different regions, and for that reason they were considered separately. The breast is frequently lighter in color while the hackle color may be either lighter or darker than the general surface color. The under color is usually considerably lighter than that of the surface.

The inheritance of the amount of black in the wing feathers was studied, and the results from the primary and secondary wing feathers were tabulated separately. In addition to the studies on plumage color the inheritance of eye color was also considered.

INHERITANCE OF BACK COLOR

Since the back color of the males averaged somewhat darker than that of the females, it was necessary to tabulate separately the results from the two sexes. Any study of back color is complicated by this sexual dimorphic condition, because a male and female of the same genetic make-up are not the same color.

The results from the matings of individuals varying in back color are shown in tables 1 and 2. In table 1 are given the mean grades of sons and daughters from varying parental grades for all surface regions. These condensed results show the general trends but are not satisfactory for genetic analyses. In table 2 is presented the distribution in the various matings of the offspring among the five grades of back color.

TABLE 2.—*Distribution of offspring and mean results from all available parental combinations of grades of plumage and eye color*

BACK PLUMAGE

Parental color grade	Distribution of daughters in color grades indicated						Distribution of sons in color grades indicated					
	1	2	3	4	5	Mean grade	1	2	3	4	5	Mean grade
♂ ♀												
5×4		16	71	72		3.35			4	57	53	4.43
5×3		21	142	63		3.19			6	99	60	4.33
5×2	1	9	35	10		2.98			3	13	18	4.44
Total or average	1	46	248	145		3.22			13	169	131	4.38
4×5		2	60	94	2	3.61		1	7	101	24	4.11
4×4	2	65	292	113	1	3.10		1	48	272	70	4.05
4×3	6	77	228	85		2.99		2	28	203	87	4.17
4×2	6	62	92	19	1	2.71	1		35	100	20	3.88
4×1		6	13	1		2.75			2	13		3.87
Total or average	14	212	685	312	4	3.07	1	4	120	689	201	4.07
3×4		15	40	13		2.97			4	39	12	4.15
3×3		8	23	4		2.89			2	14	3	4.05
Total or average		23	63	17		2.94			6	53	15	4.12

TABLE 2.—*Distribution of offspring and mean results from all available parental combinations of grades of plumage and eye color*—Continued

BREAST PLUMAGE

Parental color grade	Distribution of daughters in color grades indicated						Distribution of sons in color grades indicated					
	1	2	3	4	5	Mean grade	1	2	3	4	5	Mean grade
♂ ♀												
5×4	7	30	25	21	1	2.75	------	5	21	31	5	3.58
5×3	5	9	9	4	------	2.44	------	1	6	10	6	3.91
5×2	------	6	2	1	------	2.44	------	1	4	2	1	3.38
Total or average	12	45	36	26	1	2.66	------	7	31	43	12	3.65
4×5	------	6	25	32	------	3.41	1	2	15	17	2	3.46
4×4	17	62	102	78	2	2.95	------	24	70	99	21	3.55
4×3	27	107	96	32	1	2.52	1	25	94	78	20	3.42
4×2	50	130	89	19	------	2.27	------	45	117	86	9	3.23
4×1	8	18	11	------	------	2.08	------	11	15	4	------	2.77
Total or average	102	323	323	161	3	2.61	2	107	311	284	52	3.37
3×4	14	84	60	12	------	2.41	------	21	59	52	8	3.34
3×3	5	83	54	8	------	2.43	1	19	63	25	8	3.17
3×2	34	125	74	6	------	2.22	1	48	79	31	7	2.97
Total or average	53	292	188	26	------	2.33	2	88	201	108	23	3.15
2×4	5	32	22	6	------	2.45	1	16	27	9	2	2.91
2×3	11	45	16	------	------	2.07	------	13	18	9	------	2.90
2×2	8	20	13	1	------	2.17	------	21	13	4	------	2.55
2×1	14	3	------	------	------	1.18	------	5	2	1	------	2.50
Total or average	38	100	51	7	------	2.14	1	55	60	23	2	2.79

HACKLE PLUMAGE

5×4	------	------	11	23	------	3.68	------	1	3	11	9	4.17
5×3	------	1	33	50	1	3.60	------	1	13	46	12	3.96
5×2	------	------	7	2	------	3.22	------	------	2	5	1	3.88
Total or average	------	1	51	75	1	3.59	------	2	18	62	22	4.00
4×5	------	------	5	19	3	3.93	------	------	------	7	2	4.22
4×4	4	28	139	120	5	3.32	------	11	47	123	31	3.82
4×3	------	14	133	86	------	3.31	------	3	55	84	23	3.77
4×2	------	6	19	3	------	2.89	------	1	8	5	------	3.29
Total or average	4	48	296	228	8	3.32	------	15	110	219	56	3.79
3×5	------	------	21	18	------	3.46	------	1	15	16	------	3.47
3×4	------	12	154	118	------	3.37	------	15	84	120	29	3.66
3×3	------	27	203	83	------	3.18	------	13	117	140	26	3.60
3×2	------	13	57	30	1	3.19	------	8	29	33	1	3.38
Total or average	------	52	435	249	1	3.27	------	37	245	309	56	3.59
2×4	------	4	98	41	------	3.26	------	1	53	64	2	3.56
2×3	------	13	69	27	------	3.13	------	18	43	29	7	3.26
2×2	2	11	35	8	------	2.88	------	9	22	15	6	3.35
Total or average	2	28	202	76	------	3.14	------	28	118	108	15	3.41

TABLE 2.—*Distribution of offspring and mean results from all available parental combinations of grades of plumage and eye color*—Continued

UNDER PLUMAGE

Parental color grade	Distribution of daughters in color grades indicated						Distribution of sons in color grades indicated					
	1	2	3	4	5	Mean grade	1	2	3	4	5	Mean grade
♂ ♀												
5×4		6	7	1		2.64		2	3			2.60
5×3		14	7			2.33		4	12	2		2.89
5×2		7	5			2.42			10	1		3.09
Total or average		27	19	1		2.45		6	25	3		2.91
4×5		15	74	25		3.09		12	71	10		2.98
4×4	4	50	107	23		2.81	4	39	88	14		2.77
4×3	7	69	65	4		2.46	1	31	48	11		2.76
4×2	1	50	46	1		2.48		34	64	4		2.71
4×1	1	15	12			2.39	4	22	24	2		2.46
Total or average	13	199	304	53		2.69	9	138	295	41		2.76
3×4	2	40	73	9		2.72		12	97	7		2.96
3×3	11	83	185	15		2.69		22	137	43		3.10
3×2	11	155	160	8		2.49	1	61	170	24		2.85
Total or average	24	278	418	32		2.61	1	95	404	74		2.96
2×4		70	82	8		2.61		26	97	2		2.81
2×3		35	35	2		2.54		29	37	4		2.64
2×2	7	73	45			2.30		30	73	1		2.72
2×1		7	10			2.59		2	6			2.75
Total or average	7	185	172	10		2.50		87	213	7		2.74

BLACK IN PRIMARIES

5×4		13	39	17	6	3.21		2	11	6	27	4.26
5×3	1	43	82	15	10	2.93		3	24	22	35	4.06
5×2	8	104	105	27	6	2.68	2	47	58	69	36	3.42
5×1		6	7	2		2.73		1	5	2	1	3.33
Total or average	9	166	233	61	22	2.84	2	53	98	99	99	3.68
4×4	2	15	22	8	3	2.90		8	13	10	16	3.72
4×3	3	25	32	5	7	2.83		4	11	25	20	4.02
4×2	8	58	41	6	4	2.49	1	22	43	41	18	3.42
4×1	5	22	10	1	3	2.39		9	7	4	7	3.33
Total or average	18	120	105	20	17	2.63	1	43	74	80	61	3.61
3×4	3	20	28	14	2	2.88	2	3	6	18	18	4.00
3×3	4	44	38	12	3	2.66	1	23	21	25	17	3.39
3×2	13	101	97	15	3	2.54	5	57	52	54	26	3.20
3×1	5	9	4	1		2.05	2	7	3	3	4	3.00
Total or average	25	174	167	42	8	2.60	10	90	82	100	65	3.35
2×4		7	20	2		2.83		7	5	8	12	3.78
2×3	15	57	21	4		2.14	3	29	31	16	6	2.92
2×2	58	206	35		1	1.93	19	105	49	26	10	2.54
2×1	3	7	1			1.82		7	2	1		2.40
Total or average	76	277	77	6	1	2.04	22	148	87	51	28	2.75

TABLE 2.—*Distribution of offspring and mean results from all available parental combinations of grades of plumage and eye color*—Continued

BLACK IN SECONDARIES

Parental color grade ♂ ♀	Distribution of daughters in color grades indicated						Distribution of sons in color grades indicated					
	1	2	3	4	5	Mean grade	1	2	3	4	5	Mean grade
5×5	----	1	7	16	6	3.90	1	1	4	7	14	4.19
5×4	2	4	48	35	13	3.52	1	2	8	26	40	4.32
5×3	4	36	102	89	19	3.33	1	8	27	55	60	4.09
5×2	13	10	39	23	12	3.11	3	2	14	31	32	4.06
5×1	----	7	20	8	2	3.14	2	----	3	9	8	3.95
Total or average	19	58	216	171	52	3.35	8	13	56	128	154	4.13
4×5	4	1	16	3	8	3.31	2	----	3	3	12	4.15
4×4	4	14	75	36	5	3.18	----	3	12	45	56	4.33
4×3	29	64	143	69	14	2.92	10	23	58	89	99	3.87
4×2	16	29	51	28	5	2.82	11	14	27	34	30	3.50
4×1	32	37	36	10	4	2.30	13	14	17	28	16	3.23
Total or average	85	145	321	146	36	2.87	36	54	117	199	213	3.81
3×4	6	4	12	1	1	2.46	2	----	1	8	1	3.50
3×3	15	18	13	5	----	2.16	2	4	23	18	4	3.35
3×2	13	9	12	4	----	2.18	6	3	6	17	9	3.49
3×1	12	8	19	5	----	2.39	8	5	15	4	2	2.62
Total or average	46	39	56	15	1	2.27	18	12	45	47	16	3.22
2×5	1	3	3	----	1	2.63	1	----	3	2	5	3.91
2×4	2	6	8	4	2	2.91	2	1	8	5	8	3.67
2×3	18	20	32	7	5	2.52	7	8	17	13	16	3.38
2×2	12	16	19	2	----	2.22	6	6	7	6	4	2.86
2×1	14	12	5	3	----	1.91	9	9	3	5	4	2.53
Total or average	47	57	67	16	8	2.39	25	24	38	31	37	3.20
1×3	5	10	9	2	----	2.31	2	5	4	3	1	2.73
1×2	8	4	2	----	----	1.57	6	2	3	3	----	2.21
1×1	19	10	5	1	----	1.66	13	4	4	2	1	1.92
Total or average	32	24	16	3	----	1.87	21	13	11	8	2	2.22

EYE COLOR

6×5	1	16	22	19	7	9.23	3	13	16	3	3	8.74
6×4	----	3	6	8	1	9.33	----	3	1	2	----	8.83
Total or average	1	19	28	27	8	9.27	3	16	17	5	3	8.75
5×6	1	4	30	24	14	9.63	----	3	12	18	18	10.00
5×5	5	20	64	75	32	9.56	----	12	48	56	43	9.82
5×4	1	9	51	96	17	9.88	1	13	44	78	45	9.85
5×3	1	18	25	37	4	9.29	----	10	24	33	8	9.52
5×2	----	3	13	13	1	9.40	1	1	----	3	5	10.00
Total or average	8	54	183	245	98	9.55	2	39	123	188	119	9.80
4×6	1	15	41	22	14	9.36	1	7	20	28	15	9.69
4×5	3	29	69	76	34	9.52	1	14	53	69	26	9.64
4×4	4	37	74	82	24	9.38	4	28	54	72	22	9.44
4×3	1	15	34	20	7	9.22	1	8	29	26	13	9.55
4×2	2	5	6	2	1	8.69	----	2	6	2	2	9.33
Total or average	11	101	224	202	80	9.39	7	59	162	197	78	9.47
3×6	----	6	5	6	3	9.30	----	4	5	4	2	9.27
3×5	2	14	31	39	12	9.46	1	20	25	30	6	9.24
3×4	----	37	54	30	10	9.09	4	26	30	18	11	9.07
3×3	----	11	19	14	5	8.27	2	5	12	7	8	9.41
3×2	1	4	4	3	----	8.75	----	6	4	1	----	8.55
Total or average	3	72	113	92	30	9.24	7	61	76	60	27	9.17

The usual method of ascertaining in the fowl whether sex-linked factors are involved in a genetic make-up is to compare the female offspring from reciprocal matings. The sexual dimorphism encountered here makes this somewhat difficult. The means would indicate that males and females of the same genotype differ about one grade, the males being the higher. Selecting an average male (grade 4) and an average female (grade 3) and comparing the means when they were mated to the full range of grades of the opposite sex would supply some evidence as to whether sex-linked factors are involved. Since the female bird has only one sex chromosome and thus must receive it from her father she will show the influence of the sex-linked factors which he carries. Thus where the males are of a variable constitution, the daughters should show a greater range of variability than those from the cross where the females are of varying constitution. The mean grades of daughters from the mating of grade 3 females to the range of grades of males are no more variable than are those of daughters from the matings of grade 4 males to females of the different grades. Further evidence may be obtained from the comparison of the reciprocal mating of the most extreme—the darkest males with the lightest females and the lightest males with the darkest females. These combinations were 5 ♂ × 2 ♀ and 3 ♂ × 4 ♀, and the former had daughters averaging 2.98, and the latter 2.97 in color grade. Thus there appears to be no evidence that sex-linked factors are involved in producing the color variations on the back of the Rhode Island Red.

The rather consistent gradation of the means (for back color) shown in table 1 indicates somewhat strongly that variations in the surface color are inherited. The males used in the matings were of the grades 3, 4, and 5, while the females were distributed in all five classes. As the grade of the male decreased when mated to one grade of females, the mean of the offspring decreased. The same results were obtained from the different grades of females.

Although the evidence for heritability of the shade of red on the back appears to be good, it seems that the mode is not simple. The wide range of color grades among the off-spring in all crosses recorded in table 2 signifies that a number of determiners are probably responsible for the standard color.

INHERITANCE OF BREAST COLOR

The plumage of the breast region is usually lighter in color than that of the rest of the body (table 1). A comparison of the means of offspring from all available matings for back color and breast color shows that the males manifest a slightly greater difference in the two regions than the females.

Since the males were somewhat darker than the females with respect to breast color, the sexes were recorded separately. In table 2 the reciprocal crosses, grade 4 ♂ × grade 2 ♀ and grade 2 ♂ × grade 4 ♀, show the female offspring from the lighter males to be slightly darker than those from the darker males. Since this is the reverse of what would be expected from sex-linked factors, it may be stated that the sex chromosomes probably carry no genes affecting color in this region. There is also a slight difference in the mean of the males from these two combinations of matings, and this is not to be expected in cases of sex linkage. The difference in the means of offspring color from

these reciprocal matings is probably due to individual differences in the parent stock.

From the data in table 2 it is evident that the range of offspring from all available matings is relatively wide. In matings of grade 5 ♂ with grade 4 ♀ all five grades of female and four grades of male offspring were produced. This indicates that several factors are involved, and that many of the parents were not homozygous for the dark breast which they carried. Since the means of offspring from the different matings (table 2) seem to be lower than, rather than intermediate to, the parent grades, the major factors for light pigmentation are probably partially dominant to those for dark pigmentation.

TABLE 3.—*Coefficient of correlation of color intensity in various sections of plumage*

Sections of plumage	Number of birds	Region A		Region B		Correlation coefficient
		Mean	Standard deviation	Mean	Standard deviation	
Back (A) and breast (B)	1,022	3.11	0.691	2.41	0.835	0.787±0.008
Back (A) and hackle (B)	1,022	3.11	.691	2.24	.610	.660± .012
Back (A) and secondaries (B)	1,022	3.11	.691	2.84	1.041	−.013± .021
Primaries (A) and secondaries (B)	1,022	2.53	.903	2.84	1.041	.679+ .012

The data in table 3 show a positive correlation of 0.787 ± 0.008 between the grades of breast and back color. The probable explanation of this correlation is that the same major genetic factors control color in these two regions, although minor factors might cause some independent variation. The fact that the breast is usually lighter than other regions may be due to a general pattern factor.

INHERITANCE OF HACKLE COLOR

The difference found between the intensity of color in the hackle of the two sexes was less than that observed in the sections of the plumage previously discussed. From the values in table 2 it may be noted that when fowls in grades 4 and 5 were mated together they produced very few offspring lighter than grade 3, whereas when both parents were in grade 2 they produced several dark offspring. These results indicate that light color is dominant over dark since the heterozygotes would give the dominant color a wider range. The more restricted distribution may be the result of fewer factors being involved than in the case of the other regions studied. The inheritance of hackle color is probably dependent on more than one pair of factors, since no simple ratios can be assigned to the results.

An examination of the means from reciprocal matings, grade 5 ♂ × grade 3 ♀ and 3 ♂ × 5 ♀, or 4 ♂ × 2 ♀ and 2 ♂ × 4 ♀, show no indication of sex linkage. In one case the darker male gives the darker female offspring, and in the other case the darker male produces the lighter female offspring. These results indicate that genes in the sex chromosomes are not responsible for the variations in color of the hackle.

A positive correlation of 0.660 ± 0.012 (table 3) was found between the hackle and back color. The relatively high association of color intensity in these two regions would indicate that any existing differences are due to pattern factors. Another explanation of the correlation is that the same factors are responsible for the color of both regions and there are few modifying factors present to cause variations.

INHERITANCE OF UNDER COLOR

The study of inheritance of under color is based primarily on the red pigmentation in the fluff of the feathers on the back and does not take into consideration the black or white in this region. The variety of colors found in this part of the feather makes it very difficult to grade this region and may account for some of the irregular results obtained. The males seem to be slightly darker than the females (table 2), but there appears to be little order to the mean grade of offspring from different grades of males.

There is so little difference in average color grade from the different parental combinations that the evidence for inheritance of variations in under color is not good. These results may be due to unidentified environmental factors and also may be due to the narrow range of variation found. The narrow range in average color grade from the different parental combinations is evident from the results in table 2, there being little difference in the mean of offspring from grade 5 males and that of grade 2 males. There was a general tendency for the under color to vary with the surface color.

INHERITANCE OF BLACK IN PRIMARY AND SECONDARY WING FEATHERS

The major genetic factor considered in the inheritance of black in the primary and secondary wing feathers is the e^m factor of Dunn.[8] This factor acts by restricting the expression of melanic pigment to the extremities and is commonly known as the Columbian pattern. Dunn believes that its normal allelomorph is extended black. The variations studied here are probably due to modifying factors influencing the degree of restriction of black in the flight feathers. The amount of black in the web of the feathers of these two regions varies widely; some feathers are practically without black, while others are almost entirely black as seen in figure 1 which shows the range of the variations. The grade 6 occurred so infrequently that the few were included in grade 5 in the tables.

Upon examination of the means of offspring recorded in table 2 it is seen that there is more black in the secondaries than in the primaries. This difference may be due to a pattern factor or to a different combination of the factors affecting each region. Sexual dimorphism necessitated the recording of the sexes separately.

Most of the matings summarized in table 2 show a wide range of grades of offspring. This fact would indicate the possibility that several factors are responsible for the inheritance of black pigment in these two regions. The means of the offspring from the various matings, as recorded in table 2, are generally intermediate between the two parental grades, thus indicating a blending type of inheritance without much indication of dominance of either the lack or excess of melanic pigment. The possibility of the same factors controlling color in primaries and secondaries is supported by the correlation coefficient of 0.679 ± 0.012 between the degree of black in the two sections of the wing. The correlation-coefficient value is given in table 3.

The data in table 2 show the amount of black in the secondaries of the female offspring from the combination, grade 2 ♂ × grade 5 ♀ to be less than that from the combination, grade 5 ♂ × grade 2 ♀. This might be taken as evidence for sex linkage in the secondaries,

[8] DUNN, L. C. See footnote 4.

but it is rather doubtful that this could be the case after an examination of crosses 1 ♂×3 ♀, 3 ♂×1 ♀, 2 ♂×4 ♀, and 4 ♂×2 ♀ in which the female offspring do not seem to follow the mean of the male parent. The means of the male offspring in these reciprocal crosses differ to such an extent as to make more questionable the possibility of sex linkage. The means of female offspring from reciprocal matings 4 ♂×2 ♀, 2 ♂×4 ♀, and 1 ♂×3 ♀, 3 ♂×1 ♀ (table 2) show no indications of sex linkage in the primary wing feathers.

The means of the offspring from all mating combinations recorded in table 2 indicate that excess black in these two areas is inherited, because the means seem to recede as the mean of the mating combination is reduced. The means of the offspring have a direct relation to the grade of the male parent if a comparison is made of varying grades of males when mated to females of the same grade. The same is true if the female grade is varied while her mates' grades are held constant. The rather wide difference between the mean of offspring from the darkest and lightest males indicates the possibility of fewer factors being concerned or, at least, a more clean cut segregation of those involved.

The distribution of color grades for the offspring (table 2) includes all five grades in most cases and bears out the earlier statement concerning a wide range in the amount of black in the primaries and secondaries of different birds.

Bittenbender [9] stated that individuals carrying a dark-red color often have an excess of black in wing. This would indicate that black in wing is associated with the intensity of surface pigmentation. Table 3 data show a negative correlation of -0.013 ± 0.021 to exist between the intensity of surface pigmentation and the degree of black in secondaries. A correlation of such small magnitude is not significant and shows that there is no association between the degree of pigmentation of these two regions.

The amount of black in the wing may be controlled by factors which modify the Columbian pattern found in the Rhode Island Red, and these factors probably have nothing in common with those controlling the intensity of red in the surface.

INHERITANCE OF EYE COLOR

Upon examining the eyes of Rhode Island Red fowls, one will find all variations in color, from a light gray (grade 1) to the reddish-bay (grade 6) iris which is most desired. Differences in distribution as well as kinds of pigment in the eye made the classification of the variations difficult. The grades indicated primarily the amount of red in the iris. The eye color standards [10] show that the reduction in red color begins at the margin of the pupil and progresses toward the outer margin of the iris. Grade 1 occurred so infrequently that no provision was made for this group in the tables. Observations also indicated that there was no change in eye color associated with age. The eye color variations were not associated with any variations in plumage color.

Bond [11] in describing eye color in several breeds states that daw eye (no red) acts as a recessive to a black pigment iris in pigeons and

[9] BITTENBENDER, H. A. See footnote 3.
[10] WARREN, D. C. See footnote 6.
[11] BOND, C. J. ON CERTAIN FACTORS CONCERNED IN THE PRODUCTION OF EYE COLOUR IN BIRDS. Jour. Genetics 9: [69]-81. 1919.

fowls. Further work on the genetics of eye color in poultry is not available.

An examination of table 2 discloses no pronounced sexual dimorphism with regard to eye color. The results here are much less definite than those obtained from the study of black in flight feathers. It is also seen that there is a slight tendency for the mean grade of the offspring to vary with that of the parents. There is, however, considerable lack of consistency in the agreement. Although there is a rather wide range of eye color in the stock considered, the means of eye color for offspring from the most extreme parental combinations do not differ greatly.

The general trend of the results may be taken as evidence of some heritability of eye-color variation in the Rhode Island Red. The evidence is less definite than that found for any of the other color factors studied except that for under color. This may be taken to indicate that some environmental factors are acting to obscure the heritable tendencies. No such environmental factors were identified.

DISCUSSION OF RESULTS

It has not been possible to place the variations in plumage and eye color in the Rhode Island Red on a definite genetic factorial basis. Such results are more or less to be expected when dealing with a quantitative character of this type. The results are further complicated by the necessity of classifying the variations in arbitrary grades.

The method by which the standard color has been acquired in any breed of fowl would tend to bring about a complicated genetic constitution. The poultryman has set up an ideal and accumulated within the breed any hereditary variations which have produced a change in the direction of the ideal. This method would tend to establish in the breed a number of modifying factors. The accumulation of these factors has proceeded over a considerable period of years, and anyone who attempts to unravel the skein of germ plasm should expect to find it a much tangled one.

All the birds considered in this study had a color characteristic of the breed, and the variations considered were those which measured the closeness of approach to the ideal color. It is well known that two major factors are concerned in the production of the Rhode Island Red pattern. These are the sex-linked gold which determines the ground color, and the factor for Columbian pattern which acts in restricting the expression of black to the extremities. It is evident that we have well fixed in this breed other factors darkening the gold color, since the buff varieties, which are much lighter in color, are also known to carry the gold factor. The factors which have been considered are those affecting the intensity of the gold color, and they are not well fixed in the breed. The factors influencing the amount of black in the flight feathers are those modifying the restricting action of the factor for Columbian pattern on black.

The fact that the intensity of color in the various sections of the plumage has been considered separately does not necessarily indicate that color in these regions shows independent inheritance. The back, hackle, breast, and under surface were the sections of the plumage which showed greatest contrast in color. The general re-

sults tend to support the hypothesis that one major factor controls color in all the regions mentioned. The correlation studies showed a fairly high degree of association in the intensity of pigmentation for these sections of the plumage. The summaries of the results in all cases show the males to be darker than the females. Also wherever there was any evidence for dominance or recessiveness the lighter color appeared to be dominant. It is suggested that the difference in intensity of color in the various sections of the plumage may be due to the action of a general pattern factor in the breed.

Although the exact number of factors concerned in color inheritance in this breed could not be determined, there is definite evidence that intensity of color in the back, hackle, and breast, and the amount of black in the flight feathers are inherited. The evidence favoring the inheritance of intensity of color in the under surface of the plumage is much less definite.

In the case of the amount of black in the flight feathers there is a very close agreement in the mean grade of the parents and that of the offspring. The results seem to supply unquestionable evidence that variations in the amount of black in these feathers are inherited but also indicate that several factors are probably concerned in their transmission. Correlation studies show that there is no association between the intensity of pigmentation in the general body color and the amount of black in the wing feathers.

The variations in eye color in this breed do not show definite evidence that they are inherited. The general trend of the results seems to suggest their heritability, but the difference in results when extremes of color are mated is not great.

In all sections of plumage studied and also in eye color, the matings were of such a nature that tests could be made for evidence of sex linkage of the factors concerned. In no case is there evidence that any of the factors involved had their genes carried by the sex chromosome.

SUMMARY

Although there are differences in the shade of red color in four sections of the plumage the general surface, hackle, breast, and under surface of the Single Comb Rhode Island Red fowl, no evidence was found for important independent factors affecting color in these different regions.

Evidence was found for the heritability of the variations in intensity of pigmentation of the general surface, hackle, and breast, but the results support the view that it is a multiple-factor situation. The evidence for heritability of under color was not so definite.

Variations in amount of black in the flight feathers were found to be inherited, but the degree of black in the wings was found to be independent of the intensity of pigmentation of the general surface.

Results on the study of eye color did not seem to indicate that the variations in eye color are inherited.

Sexual dimorphism was observed in plumage-color variations, the males averaging darker than the females in all sections.

None of the characteristics studied showed any evidence that sex-linked factors are concerned.