STUDIES ON DOMINANCE AND PLEIOTROPY USING SEGREGATING INBRED LINES OF FOWL[1]

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R. A. FISHER (1930) developed a phylogenetic and statistical theory of dominance of wild type over mutants involving a selection of modifiers that shift the phenotype of the heterozygous mutant toward the wild type. The wild type has a selective advantage which also is conferred upon heterozygotes. FISHER (1934, 1935, 1938) noted that many common mutations in the domestic fowl were dominant in contrast to those of Drosophila. The fowl, therefore, provided material to test a crucial point in the dominance theory. If "domestic" dominants had evolved through artificial selection during the process of domestication, this could be demonstrated by showing that, in wild stocks not previously subjected to artificial selection, dominance is incomplete; i.e., the heterozygote is intermediate between two homozygous types.

FISHER's experiment consisted of introducing several supposedly dominant genes into a stock of wild jungle fowl. This was done by backcrossing the heterozygote five successive generations to the jungle fowl stock followed by interbreeding the heterozygotes. Thus, all three genotypes were obtained in a relatively pure jungle-fowl genetic background. Dominance was found to be incomplete in the case of three mutations influencing pigmentation. These were Barring (*B*), pile (dominant white) (*I*), and black internal pigment. In fact, barring appeared to be more nearly recessive than dominant.

Later, FISHER (1949) in his book, *Theory of Inbreeding*, suggested that segregating inbred lines might be useful in studies of dominance and linkage and that "What is needed in practice is the gene and at least one of its allelomorphs—segregating together in a uniform genetic background, and this is supplied by a segregating inbred line.—The time consumed in preparing the genetic material for making an adequate comparison is often considerable and it is a great advantage to possess stocks of prepared material available for future use."

DUNN's (1942) investigation of two reduced tail-length mutations (*T*) and (*Sd*) in the mouse is a notable example of segregating inbred lines and dominance

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modifiers. One stock which had modifiers increasing tail length for *T* also had modifiers which decreased tail-length for *Sd*. Thus, the same inbred line contained genes modifying two similar phenotypes in opposite directions. The modifiers appeared to be specific for a particular mutation rather than a general phenotype.

The objectives of the present study are: (1) to examine the dominance relationships in different genetic backgrounds of three mutant genes of the fowl; and (2) to measure the effects of the genes on body weight, egg production and egg weight.

MATERIALS AND METHODS

A. *Genes introduced:* The present study is concerned with three recognized single gene effects in the domestic fowl: dominant white, generally thought to produce the white plumage color common to White Leghorns (given the symbol *I*—Inhibitor of black pigment); Rose comb, determined by a dominant gene *R* (characterized by a low flat head appendage covered with smooth even papillae); and sex-linked Barring (*B*), which restricts the deposition of melanin to bars in the feathers that would otherwise be a solid color. The gene symbolism used is that suggested by JAAP and HOLLANDER (1954). Genes of the standard wild type are designated with a "+" superscript.

B. *General mating procedure:* Segregating inbred lines were developed by first outcrossing an already established inbred line to bring in the desired gene and then by successively backcrossing the heterozygote to the inbred. A segregating inbred line is defined as a line heterozygous for a specific single-locus character. These lines are symbolized as follows:

$$A^n \times B$$

Where A is the parent inbred line backcrossed *n* generations after outcrossing to line B to introduce the desired gene. Populations including the three genotypes are established by *inter se* matings of the segregating inbred lines. These populations were then performance tested.

C. *Genetic stocks:*

Line	*Breed*	*Date of origin*	*Estimated inbreeding coefficient*
L-9	White Leghorn	1939	93%
L-19	" "	1944	68%
L-BA	" "	1954	40%
L-HN	" "	1954	40%
L-SP	Spanish (Castellana Negra)	1954	25–30%
L-SP	" (barred)	1956	27–42%
L-WG	White Wyandott	1953	unknown

Since 1956 L-9 and L-19 have been maintained by flock matings. L-SP is a black-plumaged Spanish breed closely resembling the Black Minorca and was obtained from the University of Minnesota in 1954. They have since been maintained as a closed flock.

Seven segregating lines were formed by the backcrossing procedure already described. These are presented in Table 1. Of the seven lines, four segregated for *I*, three for *R*, and one for *B*.

D. *Statistical methods:* The quantitative traits measured on female test populations were body weight at three ages, egg production in two periods, and egg weight. Egg production was measured in Period 1 (September 6 to December 28) and in Period 2 (February 14 to April 19). The quantitative data were analyzed by the method of least squares based on the mathematical model:

$y = \mu + s_i + g_{ij} + h_k + e_{ijkm}$, where y = performance of an individual bird, μ = general population mean, s_i = effect of the ith line, g_{ij} = effect of the jth genotype within the ith line, h_k = effect of the kth hatch, e_{ijkm} = deviation of the mth bird from the mean of the ijth genotype of the kth hatch.

A within-line preliminary analysis indicated that the hatch × genotype interaction was negligible, and therefore was not included in the model. Also the hatch × line effect was assumed to be negligible.

Genotypes were analyzed on a within-line basis because of possible allelic differences between the introduced genes. Thus the genotype × line interaction is included in the genotype/line parameters and mean squares. However, preliminary inspection of the data did not indicate any genotype × line interaction.

The analysis of variance with expectations of the mean squares is:

Source	*Degrees of freedom*	*Expected mean squares*
Hatches	$h-1$	$\sigma_e^2 + k_3\,\sigma_h^2$
Lines	$s-1$	$\sigma_e^2 + k_2\,\sigma_s^2$
Genotypes/Lines	$t-1$	$\sigma_e^2 + k_1\,\sigma_{g/s}^2$
Error	$N-h-s-2$	σ_e^2

where h = the number of hatches, s = the number of lines, t = the genotype within line subclasses, and N = total number of individuals.

TABLE 1

Segregating lines formed

Segregation lines	Genes segregating	Source	Year test population formed	Genetic background
$9^4 \times$ SP	I/i^+	I from L-9; i^+ from L-SP	1959	L-9
$BA^4 \times$ SP	I/i^+	I from L-BA; i^+ from L-SP	1959	L-BA
$SP^4 \times 9$	I/i^+	I from L-9; i^+ from L-SP	1957+1959	L-SP
$SP^4 \times$ BA	I/i^+	I from L-BA; i^+ from L-SP	1957+1959	L-SP
$9^4 \times$ WG	R/r^+	R from L-WG; r^+ from L-9	1959	L-9
$19^4 \times$ WG	R/r^+	R from L-WG; r^+ from L-19	1959	L-19
$HN^4 \times$ WG	R/r^+	R from L-WG; r^+ from L-HN	1959	L-HN
SP-barred	B/b^+	B from L-SP; b^+ from L-SP	1959	L-SP

A reduced mathematical model was used in the case of sex-linked barring; since only one line was involved, no "line effect" could be estimated.

In those cases where the genotype within-line mean squares were statistically significant, the corresponding parameter estimates were tested by the *t*-test.

Adjustment of data: The necessary progeny testing to identify genotypes was conducted during the first egg production test period. Rose comb females and all Leghorn dominant white line females were mated to a recessive tester. The minimum number of phenotypically-alike test progeny sucessively produced was arbitrarily set at seven to classify a genotype as a homozygote. The maximum probability of incorrectly classifying a heterozygous individual as a homozygous is $\frac{1}{2}^7$ or 0.0078.

This procedure introduced a bias into the Period 1 egg production results because it favored the definitive classification of the better egg-producing birds. Thus, the distribution of egg production records of individuals classified as homozygotes was truncated with a deficiency of individuals in the lower production levels.

Special formulae (SMITH 1962) were developed to correct for this bias by estimating the probable number of individuals with misclassified genotypes from information on all individuals producing at least one test progeny. Least squares analyses were then conducted on the estimated populations.

RESULTS

A. *Dominant white* (I): The number of breeders in 1959 producing the segregating test populations is presented in Table 2 and the number of pullets in the 1960 segregated test populations is presented in Table 3.

Dominance: A difference in dominance expression was noted between heterozygotes originating from the Leghorn and Spanish parental lines. The heterozygotes with the Spanish background became more pigmented with successive backcrosses. The three genotypes from the *inter se matings*, I/I, I/i^+ and i^+/i^+, were respectively pure white, black-flecked and black. In the Spanish background, I is, therefore, incompletely dominant.

Heterozygotes of the first backcross to the Leghorn lines showed slight black

TABLE 2

Number of female breeders in the heterozygous lines used in 1959

Lines	Number of females	Phenotypes and genotypes	
		Males	Females
$9^4 \times$ SP	37	white I/i^+	white I/i^+
$BA^4 \times$ SP	25	white I/i^+	white I/i^+
$SP^4 \times 9$	82	black flecked I/i^+	39 black flecked I/i^+
			43 black i^+/i^+
$SP^4 \times$ BA	63	black flecked I/i^+	33 black flecked I/i^+
			30 black i^+/i^+

high gene frequency estimate of c (.93), no black-flecked birds were noted, so that I in the Leghorn Line 9 was considered completely dominant.

Segregating matings in Leghorn Line BA produced 81 white and 22 colored individuals in agreement with the expected ratio of 3 to 1. The colored individuals proved to be recessive i^+/i^+ by progeny test. However, three pure white individuals also proved to be i^+/i^+, and hence were probably recessive white (c/c). Since no black-flecked individuals were noted, I was completely dominant in Leghorn Line BA. (See Figure 1.)

Effect on quantitative traits: Table 4 shows the analyses of variance for body weight, egg production and egg weight in the Spanish lines segregating for I. Differences between genotypes within lines were statistically significant for body weight at all ages. Estimates of mean body weights for genotypes within lines are presented in Table 5.

Differences between genotypes within lines were not statistically significant for egg production or egg weight. Significant line differences were noted for eight-week weight and both egg production periods. Line $SP^4 \times 9$ laid an average of 12.4 eggs in Period 1; the greatest difference between genotypes was 2.4 eggs. Line $SP^4 \times BA$ averaged 14.4 eggs, and the greatest difference between genotypes was 2.0 eggs. Differences between genotypes in egg weight for both Spanish lines $SP^4 \times 9$ and $SP^4 \times BA$ were small. Average egg weight for these lines was 58.7 and 60.0 g, respectively.

Only pullets with genotypes classified by progeny test were used in the analyses of data from the segregating lines of Leghorn background. The analyses of variance of the quantitative traits are presented in Table 6.

Differences between genotypes within lines were not significant except for

TABLE 4

Analysis of variance of quantitative traits of Spanish lines segregating for I

		Mean squares		
	d.f.	8 weeks	20 weeks	36 weeks
Body weights (kg)				
Hatches	1	.142*	.219*	.038
Lines	1	.079†	.001	.224
Genotypes/lines	4	.026*	.137*	.285†
Error	502	.004	.052	.075
		Mean squares		
	d.f.	Period 1	Period 2	Egg weight (g)
Egg production and egg weight				
Hatches	11	7.491	1.288	4.859
Lines	1	291.860†	481.340†	53.562
Genotypes/lines	4	70.955	13.105	3.025
Error	430‡	40.369	17.670	15.289

* Significant at .05 level.
† Significant at .01 level.
‡ Error degrees of freedom for Period 2 egg production and egg weight are 407 and 253 respectively.

TABLE 5

Least squares estimates of body weight (kilograms) for the Spanish lines segregating for I

Lines	Genotype		
	I/I	*I/i*$^+$	*i*$^+$/*i*$^+$
Eight weeks			
SP^4 × 9	.689	.656*	.690†
SP^4 × BA	.636	.645	.664*†
20 weeks			
SP^4 × 9	1.592	1.642	1.714*†
SP^4 × BA	1.606	1.610	1.646
36 weeks			
SP^4 × 9	1.728	1.869*	1.914*
SP^4 × BA	1.728	1.783	1.846*

* Significantly different from *I/I*.
† Significantly different from *I/i*$^+$.

TABLE 6

Analysis of variance of the quantitative traits in the Leghorn lines segregating for I

	d.f.	Mean squares		
		8 weeks	20 weeks	36 weeks
Body weights (kg)				
Hatches	4	.0165	.466†	.056
Lines	1	.0012	3.334†	1.014†
Genotypes/lines	4	.0052	.026	.019
Error	232	.004	.017	.028
	d.f.	Mean squares		
		Period 1	Period 2	Egg weight (g)
Egg production and egg weight				
Hatches	4	116.084*	1.399	81.785†
Lines	1	1088.290†	437.858*	643.560†
Genotypes/lines	4	62.598	59.962*	5.093
Error	251‡	36.463	17.897	10.934

* Significant at .05 level.
† Significant at .01 level.
‡ Error degrees of freedom for Period 2 egg production and egg weight are 190 and 180 respectively.

Period 2 egg production, which showed a significant difference of 2.2 eggs in favor of *I/I* over *I/i*$^+$ in Line 9^4 × SP. The significant line differences are not surprising since the Leghorn inbreds were of different origin.

In body weight, Line 9^4 × SP averaged 1.238 and 1.619 kilograms, respectively, at 20 and 36 weeks. Line BA^4 × SP averaged 1.510 and 1.778 kg for the corresponding periods. The average differences between genotypes *I/I* and *i*$^+$/*i*$^+$ for both lines were 20.7, 63.5 and 9.1 grams in favor of *i*$^+$/*i*$^+$ for the three weigh periods of 8, 20 and 36 weeks, respectively. Egg production in Lines 9^4 × SP and BA^4 × SP averaged 13.39 and 18.52 eggs for Period 1, respectively. Egg weight

was 48.3 g for Line $9^4 \times$ SP and 52.8 g for Line $BA^4 \times$ SP. No effect of *I* could be demonstrated on egg production and egg weight in these Leghorn lines.

B. *Rose comb* (R): Progeny testing was required to distinguish the homozygous and heterozygous Rose comb genotypes in the segregating populations. Rose comb females were test-mated against recessive single comb male testers (r^+/r^+). The number of female heterozygous breeders was 87, 23 and 31 respectively for the lines $9^4 \times$ WG, $19^4 \times$ WG and $HN^4 \times$ WG. The classified populations for all three lines are presented in Table 7. The analysis of Period 1 egg production was corrected for bias as indicated in the METHODS section.

Matings of heterozygotes ($R/r^+ \times R/r^+$) yielded the expected three Rose comb to one single comb in each of the three lines.

Athough Rose comb remained essentially dominant with repeated backcrossing to each of the single comb lines, in the second backcross generation, the Rose comb spike became modified to a single comb-like blade. In extreme cases, even the papillae of the Rose comb were greatly reduced.

Several cross-beaked, Rose combed individuals appeared in the Rose comb segregated populations. Four cross-beak individuals reached maturity in Line $19^4 \times$ WG, of which two were classified as homozygous (R/R). In Line $HN^4 \times$ WG six had cross beaks, of which three were (R/R) and one of the heterozygous (R/r^+). Line $9^4 \times$ WG had none.

FISHER (1938) in introducing Rose comb into jungle fowl stock observed that the frontal bone between the orbits was affected. This sudden incidence of cross-beaks suggests that modifiers are present in breeds normally Rose combed, which permits normal skull development.

Table 8 presents the analyses of variance for body weights, egg production and egg weight.

No significant differences between genotypes within lines were found for any of the traits, although differences between the three inbred lines statistically differed significantly in all three traits.

C. *Sex-linked Barring* (B): The sex-linked Barred Spanish line originated from a single Barred male appearing in the SP line in 1956. The segregation of dominant sex-linked Barring from a solid black phenotype was unexpected and genetically is explained only on the basis of mutation. A remote possibility exists that Barring arose by contamination from the Barred Plymouth Rock. This seems un-

TABLE 7

Test populations for three inbred Leghorn lines segregating for Rose comb

Line	Genotype		
	R/R	*R/r+*	*r+/r+*
$9^4 \times$ WG	47	109	62
$19^4 \times$ WG	35	84	36
$HN^4 \times$ WG	20	64	46

TABLE 8

Analysis of variance of the quantitative traits measured in three inbred Leghorn lines segregating for R

		Mean squares		
	d.f.	8 weeks	20 weeks	36 weeks
Body weights (kg)				
Hatches	4	.048	.664†	.094*
Lines	2	.023	1.465†	1.041†
Genotypes/lines	6	.002	.045	.054
Error	490	.004	.025	.031
		Mean squares		
	d.f.	Period 1	Period 2	Egg weight (g)
Egg production and egg weight				
Hatches	4	68.739	29.143	97.613†
Lines	2	281.403†	113.619†	628.825†
Genotypes/lines	6	62.781	11.596	12.061
Error	521‡	31.151	17.330	16.737

* Significant at .05 level.
† Significant at .01 level.
‡ Error degrees of freedom for Period 2 egg production and egg weight are 401 and 407 respectively.

likely because the Barred progeny all showed the size and form characteristics of the Spanish breed, including an all-white ear lobe.

The Barred Spanish line was inbred with planned heterozygosis at the Barring locus in 1957 and 1958. A flock mating of 28 non-Barred females and two Barred males in 1959 produced the 1960 test flock of 58 Barred and 49 non-Barred pullets.

Table 9 presents the analyses of variance of body weights, egg production and egg weight. A statistically significant mean square was found for Barring versus non-Barring in body weight at eight weeks. The non-Barred pullets were 45.5 g heavier at eight weeks, which was statistically significant. Also the non-Barred group was 77.1 g heavier at 20 weeks and 18.1 g at 36 weeks, but these were below statistical significance. Nevertheless, the Barring gene appears to be a growth depressant in the Spanish genetic background. No important differences between genotypes in egg production and egg weight could be determined.

DISCUSSION

A single gene that governs primarily a morphological trait may influence the performance of quantitative traits if such genes are pleiotropic or if the genes for both characters are linked. Strictly speaking, the "single gene" aspect of this study may be questioned. Three generations of backcrossing to an inbred line still allow for such linkages to exist.

In the study of dominant white (*I*), two levels of dominance were found. In the Spanish segregating lines, $SP^4 \times 9$ and $SP^4 \times BA$, *I* was incompletely dominant. All three genotypes were phenotypically distinguishable, and the amount of black

TABLE 9

Analysis of variance of quantitative traits measured in the Spanish line segregating for Barring

		Mean squares		
	d.f.	8 weeks	20 weeks	36 weeks
Body weights (kg)				
Hatches	3	.013	.237†	.141
Bar *vs.* non-Bar	1	.063†	.153	.012
Error	101	.006	.043	.045
		Mean squares		
	d.f.	Period 1	Period 2	Egg weight (g)
Egg production and egg weight				
Hatches	3	182.570†	20.728	11.324
Bar *vs.* non-Bar	1	2.869	11.813	2.763
Error	49	41.110	19.964	16.553

† Significant at .01 level.

pigment in the heterozygotes increased with successive backcrosses to the Spanish.

This can be interpreted as a loss of modifiers because complete dominance characterized Leghorn backcross lines. Some possible modifiers present in the Leghorn lines, but not in the Spanish, would be sex-linked Barring and blue plumage. Hutt (1949) reported that both sex-linked Barring and blue enhances the inhibiting action of *I* on black in birds heterozygous for dominant white.

An alternative interpretation of the two levels of dominance found in this study could be based on the possible differences of the two sources of the gene *I*. Thus, the *I* from the Line 9 might not be the same allele as that from Line BA. However, since the two sources of the *I* gene gave similar results, this would seem to rule out the alternative interpretation.

The present results substantiate FISHER's (1935) conclusion that much of the dominance exhibited by mutant types is due to the selection of modifiers during the period of domestication.

A depressing effect of dominant white (*I*) on body weight was first reported by JAAP and GRIMES (1956). Since then several investigators have presented evidence of the growth depressing effect of *I* (JEROME, SLINGER, HUNTSMAN and PEPPER 1956; COLLINS and HUBBARD 1957; MERAT 1959). WILLIAMS, KRUEGER and QUISENBERRY (1959), however, reported an increase in body weight when i^+ was replaced by *I*. BLACKWOOD, BOHREN and MCKEAN (1962) found no evidence that growth rate in an inbred Leghorn line was affected by the *I* gene either through a pleiotropic action or by interaction with *E*, *B*, or *S*.

Simple linkage of small body size genes with *I* could explain the superiority of the homozygote i^+/i^+ in the Spanish backcross lines since the *I* gene came from smaller body lines. However, in the Leghorn backcross lines the superiority of the homozygote i^+/i^+ was not as evident even with the source of the i^+ allele originating from the larger body line.

When *I* was incompletely dominant, as in the Spanish genetic background, a

growth depression was noted. No growth depression was found when *I* was completely dominant as in the Leghorn lines. However, genotype differences in the segregating Leghorn lines in favor of the i^+ allele approached statistical significance at eight and 20 weeks of age. HAMILTON (1940) reported that melanophores in the embryos of both dominant and recessive white breeds of chickens have a much lower viability and higher sensitivity to adverse environmental conditions than melanophores of breeds having black plumage. Thus, if cell environment is influenced by the presence of *I*, growth depression is a possible result. In an already white or almost white breed, a suboptimal condition may already exist in the cells, and the additional effect of dominant white would not be evident.

MERAT (1961) reported that non-Barred females were significantly heavier in body weight than Barred females in some strains. In the present study growth depression seemed also to be associated with the Barring allele in the Spanish background. Since both *B* and *I* influence melanophore development, the observation of JAAP and GRIMES (1956) that melanophore development is related to growth rate is substantiated. These workers also reported that the interaction of *I* with Extension of black (*E*), Barring (*B*), and possibly Silver (S) suppressed growth which is not supported in the present study. Growth depression was found in the Spanish genetic background where only *E* and *S* were present, while no depression was found in the Leghorn background where all three genes *E*, *B*, and *S* were present.

Thus this study supports a pleiotropic action of *I* and *B* in reducing body growth and that this expression is associated with their action on the melanophores.

SUMMARY

Marker genes segregating in inbred lines were used to study dominance and interactions on quantitative traits. The gene loci studied were dominant white (*I*), Rose comb (*R*) and sex-linked Barring (*B*). The quantitative traits were body weight, egg production and egg weight.

Segregating inbred lines were produced by outcrossing an already established inbred line to bring in a desired gene and backcrossing the heterozygote in three successive generations. By this procedure each particular locus was kept in a heterozygous condition and at the same time the genetic contribution of the inbred line was increased in each successive backcross. The three genotypes for each locus were obtained by *inter se* matings of the heterozygotes in the fourth generation. Individuals of these genotypes were then compared on the basis of the quantitative traits.

Four segregating dominant white lines were produced from Leghorn × Spanish crossbred foundation stock. The parental lines were Leghorn inbred Lines 9 and BA and one Spanish line (SP). Two of the segregating lines differed in Leghorn genetic background, and two had the same genetic background (Spanish), but differed as to source of *I* genes.

In the Spanish background *I* was incompletely dominant and all three geno-

types were phenotypically distinguishable. In each of the Leghorn backgrounds *I* was completely dominant, for progeny testing was required to identify the heterozygote. *I* significantly depressed growth in the Spanish lines, but not in the Leghorn lines.

The Rose comb gene (*R*) was introduced into the three Leghorn inbred Lines 9, 19, and HN, from which segregating populations were obtained. In each line Rose comb remained essentially dominant after three backcrosses but the spike of the Rose comb became modified into a blade. Genotype differences at the Rose comb locus appear not to influence the quantitative traits measured.

The sex-linked Barring gene (*B*) was also tested for its possible influence on quantitative traits in the Spanish line. The non-Barred pullets were consistently heavier in body weight than the Barred pullets. Differences in egg production and egg weight were not statistically significant.

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