

GENETIC AND ENVIRONMENTAL EFFECTS ON BODY  
MEASUREMENTS IN BROILER CHICKENS

by

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## INTRODUCTION

The development of population genetics has made it possible for the practicing breeder to be more objective in choosing between various breeding plans. To exercise this choice, the breeder requires information about the extent and causes of variation in traits or characters of concern to him.

A primary proposition underlying the theory of population genetics is that variation among individuals in a bi-parental population can be ascribed to effects of heredity and environment, both independently and jointly.

As breeders are generally interested in considering many traits in their breeding program, relationships among these must also be considered. Correlations or covariance among traits can be ascribed to effects of heredity and environment in the same way that variance in traits can be ascribed to effects of heredity and environment.

Although there have been many quantitative studies concerning the influence of heredity and environment on variability in traits of economic importance in the fowl, only a few studies dealing with the genetic relationships among traits have been reported. Likewise, few studies concerning the interactions between heredity and environment have been undertaken. If such interactions exist and are large, they must be considered in formulating an efficient breeding program.

There is an increasing trend in the poultry industry to breed separate strains of chickens for meat or for egg production, although each has problems not entirely unrelated to the other. The breeder of meat birds,

although he must place primary emphasis on such traits as growth and carcass quality, cannot entirely ignore egg production characteristics, as they contribute to the reproductive efficiency of his stock.

The present study is concerned primarily with traits of importance in poultry meat production. The data were obtained from a closed flock bred largely for its meat production qualities.

The objectives in this study are:

- (a) To obtain heritability estimates of traits having possible importance in breeding for meat production.
- (b) To obtain estimates of phenotypic and genetic correlations between traits.
- (c) To estimate hatch effects, location effects and any interactions between these and hereditary effects.
- (d) To compare the efficiency of index selection with individual selection for these traits, and to determine the expected genetic gain for the more important traits under certain specified conditions.

## LITERATURE REVIEW

## Growth

It is well known that body weight or growth is influenced by numerous environmental factors such as crowding, chilling or excessive heat during the brooding and growing period, types of brooding, disease and nutrition. The influence of these factors is often more marked in the early stages of growth. Kempster (1938), Asmundson and Lerner (1933), Heuser and Norris (1934) and others have shown that compensatory growth often takes place.

Hatch effects on growth have been reported by a number of investigators. Hays and Sanborn (1929), Asmundson and Lerner (1933) and Kempster (1938) have reported early hatched chicks grow faster than late hatched ones. Kempster (1938) concluded that weight differences between early and late hatched chickens were mainly due to temperature differences, with high temperatures tending to retard growth. Goodman and Godfrey (1954) in a study of body weight of broilers, found that 11 percent of the variance in weight at 9 weeks of age was due to hatch effects. Brant (1951) reported that the differences in early growth between hatches were greater than the differences between the breeds and strains used.

Maternal effects on body weight in White Leghorns at 22 weeks of age were reported by Hazel and Lamoreux (1947). Lerner and Cruden (1951) also concluded that body weight in adult White Leghorns exhibited maternal effects.

Two specific mutations affecting body weight in the fowl were listed by Hutt (1949). The mutants in both cases were dwarfs and one was sex-linked. Jull (1952) and Hutt (1949) have reviewed a number of studies that have shown sex-linked effects on body size in the fowl. In all cases, however, in which sex-linked effects have been reported, the studies have been made on crosses involving bantam breeds of fowl.

Heritability estimates for body weight in the fowl have been reported by numerous workers. Since the number of estimates are extensive, they have been presented in Table 1. Estimates in the table are listed according to age groups as follows: 6-week, 8 to 12-week (approximate broiler age), 20 to 24-week (which approximates housing body weight) and 52-week or adult body weight.

No particular trend in heritability, which might be associated with age, is indicated from these studies. On the other hand, a consistent difference between methods of estimation is evident. In almost all cases heritability estimates based on the sire component of variance alone are lower than the comparable estimate from the full sib component. Moreover, estimates based on intra-sire regression are generally lower than those based on the method of intra-class correlation among full sibs.

Relationships between body weights at various ages have been studied by a number of early workers--especially the relationship between early growth and adult body size on an interbreed basis. Jaap and Morris (1937) concluded that growth rate to 8 weeks of age was not related to final body weight. Waters (1937) also concluded that early growth was not a criterion of adult body size. Lerner and Asmundson (1938), however, have shown that



Table 1. Heritability estimates (literature)

Reference	Method				
	4S	4D	2(S+D)	2bo(D)	Other
<u>6-Week Body Weight</u>					
El-Ibiary and Shaffner, 1951 M	.13		.38		
F	.14		.28		
Martin <u>et al.</u> , 1953					.30
<u>8 to 12-Week Body Weight</u>					
Brunson <u>et al.</u> , 1955					.45
Dillard <u>et al.</u> , 1953			.34	.32	
El-Ibiary and Shaffner, 1951 M	.13		.21		
F	.26		.54		
Fagan, 1949	.35		.50	.42	
Glazener <u>et al.</u> , 1951		.68			
Godfrey and Goodman, 1956 M	.36	.59	.47	.42	
F	.26	.71	.48	.51	
Hurry and Nordskog, 1953			.33		
Krueger <u>et al.</u> , 1952			.46	.33	
Lankford and McClung, 1952	.27	.66	.47		
Lerner <u>et al.</u> , 1947	.42	.60	.51		
Martin <u>et al.</u> , 1953					.29
Peeler <u>et al.</u> , 1955	.29		.38	.15	
Wyatt, 1954			.46	.40	
<u>20 to 24-Week Body Weight</u>					
Hazel and Lamoreux, 1947	.32				
Krueger <u>et al.</u> , 1952			.43	.32	

Table 1. (Continued)

Reference	Method				
	LS	LD	2(S+D)	2bo(D)	Other
<u>20 to 24-Week Body Weight</u>					
Wyatt, 1954			.31	.18	
<u>52-Week or Adult Body Weight</u>					
Lerner and Cruden, 1951	.17		.47	.80	.49
Shoffner and Sloan, 1948				.75	
Wyatt, 1954			.65		
<u>Breast Width</u>					
Dillard <u>et al.</u> , 1953			.21	.12	
Lerner <u>et al.</u> , 1947	.13	.29	.21		
<u>Breast Angle</u>					
Brunson <u>et al.</u> , 1955					.46
Godfrey and Goodman, 1956 M	.40	.50	.45	.36	
F	.49	.44	.47	.46	
<u>Body Depth</u>					
El-Ibiary and Shaffner, 1951 M	.09		.24		
F	.14		.63		
<u>Keel Length</u>					
Dillard <u>et al.</u> , 1953			.49	.48	
El-Ibiary and Shaffner, 1951 M	.22		.45		
F	.32		.30		
Lerner <u>et al.</u> , 1947	.50	.17	.34		

Table 1. (Continued)

Reference	Method				
	4S	4D	2(S+D)	2bo(D)	Other
<u>Shank Length</u>					
El-Ibiary and Shaffner, 1951	M	.03	.16		
	F	.09	.51		
Lerner <u>et al.</u> , 1947		.50	.48	.49	
Lerner and Dempster, 1951			.35	.44	
<u>Sexual Maturity</u>					
Dillard <u>et al.</u> , 1953			.25	.33	
Farnsworth and Nordskog, 1955			.40		
Hazel and Lamoreux, 1947		.27			
King and Henderson, 1954b			.52	.26	
Krueger <u>et al.</u> , 1952			.20	.07	
Lerner and Cruden, 1951		.24	.31	.35	
Peeler <u>et al.</u> , 1955		.21	.39	.40	
Shoffner and Sloan, 1948				.26	
<u>Egg Production (Hen-Housed Basis)</u>					
Dillard <u>et al.</u> , 1953			.12	.20	
King and Henderson, 1954b			.20		
Lerner, 1950			.05		

such a relationship may or may not be demonstrated depending on the data and circumstances used for the purpose. On an intrabreed basis Schnetzler (1936) reported phenotypic correlations between 8 and 12-week body weights and body weight at maturity in a strain of Barred Rocks of .29 and .39, respectively.

Reported genetic correlations between body weights at different ages have been listed in Table 2. In these studies the correlations are between body weights of birds not widely divergent in age and consequently are of a relatively high order.

Relationships between body weight and other traits have been reported by a number of investigators. Rate of feathering has been reported by Warren and Payne (1945) to be associated with growth. These workers found that birds showing rapid feathering were consistently heavier at 12 weeks of age than slow feathering birds. Jull (1952) and Hutt (1949) have reviewed a number of other reports where rate of feathering and body weight were found to be correlated, although as pointed out by Hutt, these correlations were not very high.

Jaap and Grimes (1956) and Jerome et al. (1956) reported that genes or mutations affecting plumage color may influence early body weight.

Genetic correlations between body weight and other traits in the fowl have been listed in Table 2. The correlations between body weight and other body or physical measurements, with the exception of breast width, are of a high order. Correlations with sexual maturity are of a relatively low order and inconsistent. The single reported estimate of the correlation between body weight and the production index is low and negative.

Table 2. Estimates of genetic correlations (literature)

Reference	Traits correlated	Estimate
<u>Body Weight</u>		
Martin <u>et al.</u> , 1953	Body weight (broiler age) x 6-week body weight	.92
Krueger <u>et al.</u> , 1952	x housing body weight	.83
Dillard <u>et al.</u> , 1953	x breast width	.15
Lerner <u>et al.</u> , 1947		.10
Godfrey and Goodman, 1956	x breast angle	.50
Dillard <u>et al.</u> , 1953	x keel length	.57
Lerner <u>et al.</u> , 1947		.79
Lerner <u>et al.</u> , 1947	x shank length	.87
Dillard <u>et al.</u> , 1953	x sexual maturity	-.10
Peeler <u>et al.</u> , 1955		.29
Krueger <u>et al.</u> , 1952		-.39
Dillard <u>et al.</u> , 1953	x production index	-.17
Wyatt, 1954	Housing body weight x mature body weight	.79
Hazel and Lamoreux, 1947	x sexual maturity	-.44
Krueger <u>et al.</u> , 1952		-.29

Table 2. (Continued)

Reference	Traits correlated	Estimate
Lerner and Cruden, 1951	Mature body weight x sexual maturity	.06
<u>Body Measurements</u>		
Dillard <u>et al.</u> , 1953	Breast width x keel length	-.05
Lerner <u>et al.</u> , 1947		-.08
Lerner <u>et al.</u> , 1947	x shank length	.14
Dillard <u>et al.</u> , 1953	x sexual maturity	.03
Dillard <u>et al.</u> , 1953	x production index	.01
Lerner <u>et al.</u> , 1947	Keel length x shank length	.71
Dillard <u>et al.</u> , 1953	x sexual maturity	-.14
Dillard <u>et al.</u> , 1953	x production index	.10
<u>Production Traits</u>		
Dillard <u>et al.</u> , 1953	Sexual maturity x production index	-.22

## Body Measurements

Apart from studies of growth, per se, body or physical measurements have been secured in studies on the fowl for various reasons. Some of the earlier investigators were chiefly concerned with the relationship between physical measurements and reproductive performance (mainly egg production). Many of these studies have been reviewed by Jull (1940, 1952) and by Hutt (1949). Although numerous correlations have been reported, they have been of a low magnitude.

From the standpoint of meat production in the fowl, body measurements have been used extensively to describe conformation. They have also been used in studies of meat yield.

It is well known that breed differences exist in body conformation. Various attempts have been made by investigators to describe or measure conformation objectively for both market and breeding purposes. Maw and Maw (1938) using photographs of Barred Rock sires and male progenies showed that there was some correlation in visual body shape between the sire and his progeny. Jaap and Penquite (1938) suggested various ratios of linear skeletal measurements to body weight as criteria of conformation. Jaap and Thompson (1940) reported significant differences between breeds, using these ratios as criteria of conformation. However, neither Scott (1940) nor Poley et al. (1940) found these ratios to be highly correlated with visual alignment grades of conformation. Frischknecht and Jull (1946) found the correlation between market grade and the ratio of shank length to body weight, one of the ratios proposed by Jaap and Penquite, to be of

a very low order.

Dolecek et al. (1941) suggested the use of an index involving length, width and depth of breast to describe carcass quality. These workers found this index to be highly correlated with visual alignment grade.

Lerner (1941, 1943) criticized the use of ratios as indices of conformation because the growth of the parts involved is not isometric. Lerner (1943) reported on a selection experiment in which the objective was to modify or change the shank length/body weight ratio. Selections were made on the basis of calculated growth constants. After four generations of selection no difference was observed in the growth ratios between the two selected lines. Kidwell et al. (1952) suggested that Lerner's failure to modify the growth ratios may have been the result of his use of body weight, per se, as a standard of body size. These workers suggested that relatively large measurement errors including random fluctuations, might be involved in body weight data. They concluded that these errors would serve to increase the environmental portion of the variance so that the constants derived may not have been sufficiently accurate for selection purposes.

Kidwell et al. (1952) used heart girth as a standard of body size in their study on Hereford cattle. They considered the heritabilities of various constants in Huxley's allometric equation to be of such a magnitude that conformation might be changed in a specific manner by selection for desired values of the parameters.

Various other studies in poultry have indicated that relative growth of the various parts or dimensions may be altered by selection. Wright (1932) conducted an analysis of the data presented by Dunn (1926) on



White Leghorns, and concluded that size factors having general effects were important, but that in addition, other specific factors affect the dimensions of the head and still others the legs. Kopec (1926, 1927) found certain dimensions of the body to be inherited independently of others.

Blow and Glazener (1952) stated that conformation and meat quality in broilers is chiefly a question of fleshing or breast development. Although various techniques for measuring breast development have been proposed, unfortunately no reports are available comparing these techniques with either visual impressions of quality or commercial grades. Bird (1948) designed an instrument to take breast width at  $1/5$  of body depth. Asmundson and Lerner (1951) fitted solder wire to the breast. These workers have also suggested taking direct readings with calipers. A breast angle meter designed at the University of West Virginia was used by Clark and Cunningham (1949).

McNally and Spicknall (1949) reported linear relationships between meat yield and live body weight in Rhode Island Red broilers, fryers and light roasters. Jaap (1941), Stotts and Darrow (1952) and Hathaway et al. (1953) presented evidence to show that the Cornish breed, and crossbreeds from Cornish, yield a greater percentage of edible meat than other breeds tested. Frischknecht and Jull (1946) obtained correlations between various body measurements and yield of breast meat. They found live weight to be more highly correlated with breast meat than any other single index or measurement. They also found the correlations between various breast measurements and amount of breast meat to be somewhat lower, in general,

than correlations between other body measurements and amount of breast meat. The correlations between market grade and breast measurements were slightly higher, however, than those between grade and other body measurements. Maw and Maw (1939) reported the correlations between various body measurements, not including breast measurements, and edible flesh to be low.

Blow and Glazener (1952) compared four methods of measuring breast development for their predictive value in determining breast meat yield. The four methods included width of breast using vernier calipers, impressions with wire solder, angle of the slope of the breast, and the instrument designed by Bird (1948). These workers found that body weight accounted for most of the variance in breast meat yield. The amount of the variance accounted for by the breast measurement depended on the breast measurement used. Cross-sectional area obtained with the wire solder accounted for 11 percent of the variance, the highest of the four methods. Breast width accounted for almost as much as cross-sectional area, while breast angle and the Bird index accounted for very little of the variance. These workers concluded that breast measurement with calipers was the most practical technique. Newell and Godfrey (1954) reported, however, that the use of a breast angle meter increased the precision of predicting meat yield by 7 to 8 percent. The instrument used by these workers was slightly different than that employed by Blow and Glazener.

Heritability estimates reported for different body measurements are presented in Table 1. The number of studies in which heritabilities for body measurements have been reported is not very great. No reports are available in which heritabilities of breast fleshing measurements, obtained

by different techniques, are compared. The two heritability estimates reported for breast width are both .21. Heritability estimates for skeletal measurements are somewhat higher than those for breast width and are approximately of the same order as those for body weight. Although as yet few estimates have been reported for body measurements, it appears that like those for body weight, different methods of estimation give different results.

Numerous studies have been made on the phenotypic correlations among various body measurements including body weight. Many of the studies have been reviewed by Jull (1940, 1952), Hutt (1949) and by Gilbreath and Upp (1952). In general, most of these studies have shown the correlations between fleshing measurements and skeletal measurements or body weight to be moderately low. On the other hand, correlations between different skeletal measurements have been shown to be of a relatively high order.

Reports of genetic correlations between various body measurements in the fowl are few. Those which have been reported are summarized in Table 2. The genetic correlations between breast width and skeletal measurements are low. Both estimates reported for keel length and breast width are negative. Correlations between skeletal measurements and body weight are high, while the genetic correlations between body measurements and sexual maturity and the production index are low.

#### Sexual Maturity and Production

Heritability estimates for sexual maturity and the production index are presented along with those for other traits in Table 1. Few estimates

are yet available for the production index. The estimates indicate fairly low heritabilities for this trait. On the other hand, heritability estimates for sexual maturity are more numerous and of a higher order than those for the production index.

Genetic correlations involving sexual maturity and the production index reported in the literature are given in Table 2. Few genetic correlations have been reported between these production traits and body weight or body measurements, although a large number of phenotypic correlations have been reported (Jull, 1940, 1952; Hutt, 1949). Estimates of genetic correlation between the production index and breast width and keel length are of a low order. Genetic correlations between sexual maturity and body weight are of higher order and both estimates reported are negative.

#### Genotype-Environment Interactions

Many studies in poultry have revealed the presence of genotype-environment interactions. Different genotypes have been shown to respond differently to nutritional deficiencies (Hutt, 1949 and Howes and Hutt, 1952) to disease and parasites (Scholes and Hutt, 1942; Ackert et al., 1935; Lerner et al., 1950; Edgar et al., 1951 and Rosenberg et al., 1951) and to temperature stress (Hutt, 1938 and Fox, 1951).

Genotype-environment interactions involving sexual maturity have been reported by Osborne (1951) and by Skaller and Sheldon (1955). Merritt and Gowe (1956) reported a significant interaction between strains and farms for 6-week body weight and 10-week breast angle, although no interaction

was found in this study for 10-week body weight, nor for keel or shank length. Johnson (1955) reported a significant interaction between sire groups and hatching date for body weight in turkeys.

Gowe (1955) reported a highly significant interaction between strains and locations (floor pens and battery) with respect to survivor egg production and March body weight, but found no evidence of an interaction for hen-housed egg production, sexual maturity, egg weight or mortality. Gutteridge and O'Neil (1942a, 1942b) did not find significant interactions between strains and farms for body weight or egg production.

Gowe and Wakely (1954) reported on the performance of full-sibs on test at different farms. These workers found no evidence of any genotype-environment interactions for egg production although these authors, as well as others, found significant location effects on egg production and other traits.

## STATISTICAL PROCEDURES

## Mathematical Models

Components of variance and covariance used in the estimation of heritabilities and correlations were obtained from the hierarchal type of analysis of variance.

Three mathematical models were used for purposes of obtaining components of variance for heritability estimates (Models 1, 2 and 3) while only two (Models 1 and 2) were used for estimating components of covariance for correlation estimates.

Model 1

For the data involving more than one farm (Hatches 3 and 4 in the study), the following linear model was used:

$$Y_{jklm} = \mu + f_j + s_{jk} + d_{jkl} + e_{jklm},$$

where  $Y_{jklm}$  is the observation on the  $m^{\text{th}}$  progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire at the  $j^{\text{th}}$  farm. The quantity  $\mu$  is the progeny mean and is common to all observations,  $f_j$  is common to all progeny of the  $j^{\text{th}}$  farm,  $s_{jk}$  is common to all observations on progeny of the  $k^{\text{th}}$  sire at the  $j^{\text{th}}$  farm and  $d_{jkl}$  is common to all observations of progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire at the  $j^{\text{th}}$  farm. The quantity  $e_{jklm}$  is a random element peculiar to each observation.

Although in these data farms are, in effect, factorially arranged whereas the other elements are hierarchal, this model is satisfactory for estimation of the components of variance (King and Henderson, 1954a).

Model 2

For the data involving only one farm (Hatches 1 and 2) the following linear model was used:

$$Y_{klm} = \mu + s_k + d_{kl} + e_{klm}.$$

Model 3

For the same data analyzed under Model 2 (Hatches 1 and 2) a linear model containing an element for hatches was used. This model is:

$$Y_{iklm} = \mu + h_i + s_{ik} + d_{ikl} + e_{iklm}.$$

In Model 2,  $Y_{klm}$  is the observation on the  $m^{\text{th}}$  progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire.

In Model 3,  $Y_{iklm}$  is the observation on the  $m^{\text{th}}$  progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire in the  $i^{\text{th}}$  hatch. In these data hatches are factorially arranged, although for estimation of the components of variance the hierarchical type of classification was used.

Model 4

In addition to the foregoing models, which were used to obtain components of variance and covariance for estimating heritabilities and correlations, a fourth model was used to obtain components of variance of all main effects and interactions. This model takes into account the factorial arrangement of hatches and farms in the data (Hatches 3 and 4). This model is:

$$Y_{ijk lm} = \mu + h_i + f_j + s_k + d_{kl} + (hf)_{ij} + (hs)_{ik} + (fs)_{jk} + (fd)_{jkl} + (hfs)_{ijk} + (hfd)_{ijkl} + e_{ijk lm},$$

where  $Y_{ijk lm}$  is the observation on the  $m^{\text{th}}$  progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire at the  $j^{\text{th}}$  farm in the  $i^{\text{th}}$  hatch. The quantity  $\mu$  is the

progeny mean and is common to all observations. The quantity  $h_i$  is common to all progeny in the  $i^{\text{th}}$  hatch;  $f_j$  to all progeny at the  $j^{\text{th}}$  farm;  $s_k$  to all progeny of the  $k^{\text{th}}$  sire;  $d_{kl}$  to all progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire;  $(hf)_{ij}$  to all progeny in the  $i^{\text{th}}$  hatch and the  $j^{\text{th}}$  farm;  $(hs)_{ik}$  to all progeny in the  $i^{\text{th}}$  hatch with the  $k^{\text{th}}$  sire;  $(fs)_{jk}$  to all progeny at the  $j^{\text{th}}$  farm and the  $k^{\text{th}}$  sire;  $(fd)_{ikl}$  to all progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire at the  $i^{\text{th}}$  farm;  $(hfs)_{ijk}$  to all progeny of the  $k^{\text{th}}$  sire at the  $j^{\text{th}}$  farm in the  $i^{\text{th}}$  hatch and  $(hfd)_{ijkl}$  to all progeny of the  $l^{\text{th}}$  dam mated to the  $k^{\text{th}}$  sire at the  $j^{\text{th}}$  farm in the  $i^{\text{th}}$  hatch. The quantity  $e_{ijklm}$  is a random element peculiar to each progeny.

In all models, the assumption is that except for  $\mu$ , all elements are uncorrelated variables with means zero and variances of the  $h_i$ 's equal to  $\sigma_h^2$ , etc., of the  $(hf)_{ij}$ 's equal to  $\sigma_{hf}^2$ , etc.

The analysis of variance used for estimating components of variance and covariance to obtain heritabilities and correlations is presented in Table 3. The model on which this analysis is based is Model 1.

In Model 1 it is not necessary to assume that the  $f_j$ 's (farms) are random variables in order to estimate Q, D and S. This would apply to the  $h_i$ 's (hatches) in Model 3 (King and Henderson, 1954a).

The  $k$  values in Table 3 are obtained as follows:

$$\begin{aligned} k_1 &= \sum_j \sum_k \frac{\sum_l n_{jkl}^2}{n_{jk.}} \\ k_2 &= \sum_j \frac{\sum_k n_{jk.}^2}{n_{j..}} \\ k_3 &= \sum_j \frac{\sum_k \sum_l n_{jkl}^2}{n_{j..}} \end{aligned}$$



Table 3. Analysis of variance (Model 1)

Source of variation	d.f. <sup>a</sup>	Sum of <sup>b</sup> squares	Expected sum of squares <sup>c</sup>
Total	N	T	
Correction term	1	C.T.	
Among farms	f-1	A-C.T.	
Among sires w/i farms	s-f	B-A	$(s-f)Q + (k_1-k_3)D + (N-k_2)S$
Among dams w/i sires w/i farms	d-s	C-B	$(d-s)Q + (N-k_1)D$
Among full sibs w/i farms	N-d	T-C	$(N-d)Q$

- <sup>a</sup> N = total number of individuals  
 f = number of farms  
 s = number of sire by farm subclasses  
 d = number of dam by farm subclasses
- <sup>b</sup> T = total sum of squares  
 C.T. = correction term  
 A = uncorrected farm sum of squares  
 B = uncorrected sire by farm sum of squares  
 C = uncorrected dam by farm sum of squares
- <sup>c</sup> Q = component of variance between full sibs  
 D = component of variance between dams  
 S = component of variance between sires

The method of analysis for estimating components of variance for the factorially arranged but unequal subclass case has been outlined in detail by Henderson (1953). As Model 4 involves both a factorial and hierarchal classification of the data, it was thought of interest to first work out the expectation of the mean squares for the equal subclass case (see Appendix, Table 14).

For the unequal subclass case the method consists of substituting for the Y's their corresponding linear models, then obtaining the expectation of the sum of squares. These expectations are equated to the computed sum of squares and solved for the unknown variances.

The coefficients of the variance components in the expected sum of squares are presented in Table 4.

To illustrate the computations, the coefficient  $K_{40}$  is derived as follows:

$$\begin{aligned}
 E \sum_i \sum_j \sum_k \frac{Y_{ijk..}^2}{n_{ijk.}} &= \sum_i \sum_j \sum_k E \frac{Y_{ijk..}^2}{n_{ijk.}} \\
 &= \sum_i \sum_j \sum_k E \left[ n_{ijk.} \mu + n_{ijk.} h_i + \dots + n_{ijk.} d_1 \right. \\
 &\quad \left. + n_{ijk.} d_2 + \dots + \sum_l \sum_m e_{ijklm} \right]^2 / n_{ijk.} \\
 &= \sum_i \sum_j \sum_k E \left[ n_{ijk.}^2 \mu^2 + n_{ijk.}^2 h_i^2 + \dots + n_{ijk.}^2 d_1^2 \right. \\
 &\quad \left. + n_{ijk.}^2 d_2^2 + \dots + \sum_l \sum_m e_{ijklm}^2 + \right. \\
 &\quad \left. \text{cross products with zero expectation} \right] / n_{ijk.} \\
 &= \sum_i \sum_j \sum_k \left[ n_{ijk.}^2 \mu^2 + n_{ijk.}^2 \sigma_h^2 + \dots + n_{ijk.}^2 \sigma_d^2 \right. \\
 &\quad \left. + n_{ijk.}^2 \sigma_d^2 + \dots + \sum_l \sum_m e_{ijklm}^2 \right] / n_{ijk.} \\
 &= N \mu^2 + N \sigma_h^2 + \dots + \sum_i \sum_j \sum_k \frac{\sum_l \sum_m e_{ijklm}^2}{n_{ijk.}} \\
 &\quad + \dots + \sum_i \sum_j \sum_k \sum_l \sum_m e_{ijklm}^2
 \end{aligned}$$

$$\text{where } K_{40} = \sum_i \sum_j \sum_k \frac{\sum_l \sum_m e_{ijklm}^2}{n_{ijk.}}$$

Table 4. Coefficients of the variance components in the expected sum of squares (Model 4)

Sum of squares	$\mu^2$	$\sigma^2_h$	$\sigma^2_f$	$\sigma^2_s$	$\sigma^2_d$	$\sigma^2_{hf}$	$\sigma^2_{hs}$	$\sigma^2_{hd}$	$\sigma^2_{fs}$	$\sigma^2_{fd}$	$\sigma^2_{hfs}$	$\sigma^2_{hfd}$	$\sigma^2_e$
HATCH	N	N	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	K <sub>1</sub>	K <sub>2</sub>	K <sub>3</sub>	K <sub>4</sub>	K <sub>5</sub>	K <sub>4</sub>	K <sub>5</sub>	K <sub>6</sub>
FARM	N	K <sub>7</sub>	N	K <sub>8</sub>	K <sub>9</sub>	K <sub>7</sub>	K <sub>10</sub>	K <sub>11</sub>	K <sub>8</sub>	K <sub>9</sub>	K <sub>10</sub>	K <sub>11</sub>	K <sub>12</sub>
SOIL	N	K <sub>13</sub>	K <sub>14</sub>	N	K <sub>15</sub>	K <sub>16</sub>	K <sub>13</sub>	K <sub>17</sub>	K <sub>14</sub>	K <sub>18</sub>	K <sub>16</sub>	K <sub>19</sub>	K <sub>20</sub>
DAM	N	K <sub>21</sub>	K <sub>22</sub>	N	N	K <sub>23</sub>	K <sub>21</sub>	K <sub>21</sub>	K <sub>22</sub>	K <sub>22</sub>	K <sub>23</sub>	K <sub>23</sub>	K <sub>24</sub>
H X F	N	N	N	K <sub>25</sub>	K <sub>26</sub>	N	K <sub>25</sub>	K <sub>26</sub>	K <sub>25</sub>	K <sub>26</sub>	K <sub>25</sub>	K <sub>26</sub>	K <sub>27</sub>
H X S	N	N	K <sub>28</sub>	N	K <sub>29</sub>	K <sub>28</sub>	N	K <sub>29</sub>	K <sub>28</sub>	K <sub>30</sub>	K <sub>28</sub>	K <sub>30</sub>	K <sub>31</sub>
H X D	N	N	K <sub>32</sub>	N	N	K <sub>32</sub>	N	N	K <sub>32</sub>	K <sub>32</sub>	K <sub>32</sub>	K <sub>32</sub>	K <sub>33</sub>
F X S	N	K <sub>34</sub>	N	N	K <sub>35</sub>	K <sub>34</sub>	K <sub>34</sub>	K <sub>36</sub>	N	K <sub>35</sub>	K <sub>34</sub>	K <sub>36</sub>	K <sub>37</sub>
F X D	N	K <sub>38</sub>	N	N	N	K <sub>38</sub>	K <sub>38</sub>	K <sub>38</sub>	N	N	K <sub>38</sub>	K <sub>38</sub>	K <sub>39</sub>
H X F X S	N	N	N	N	K <sub>40</sub>	N	N	K <sub>40</sub>	N	K <sub>40</sub>	N	K <sub>40</sub>	K <sub>41</sub>
H X F X D	N	N	N	N	N	N	N	N	N	N	N	N	K <sub>42</sub>
C.T.	N	K <sub>43</sub>	K <sub>44</sub>	K <sub>45</sub>	K <sub>46</sub>	K <sub>47</sub>	K <sub>48</sub>	K <sub>49</sub>	K <sub>50</sub>	K <sub>51</sub>	K <sub>52</sub>	K <sub>53</sub>	1
TOTAL	N	N	N	N	N	N	N	N	N	N	N	N	N

In Table 4, the coefficients in the last column associated with namely,  $K_6$ ,  $K_{12}$ ,  $K_{20}$ ,  $K_{24}$ ,  $K_{27}$ ,  $K_{31}$ ,  $K_{33}$ ,  $K_{37}$ ,  $K_{39}$ ,  $K_{41}$ , and  $K_{42}$  are the number of filled subclasses for the various classifications (see Table C for the actual values of these coefficients in this study).

Equating the expected sums of squares in terms of components to the corresponding computed sums of squares gives 13 equations. Subtracting the equation (due to  $u$ ) for the correction term from each of the other equations leaves 12 equations. The unknown in these equations are the 12 variance components corresponding to the 12 elements in the model.

These 12 equations were solved by the use of matrix algebra as follows:

$$A B = G$$

$$A^{-1} A B = A^{-1} G$$

since

$$A^{-1} A = I$$

therefore

$$B = A^{-1} G$$

where  $A$  = the matrix of coefficients (K values),  $^{12} \times 12$  non-symmetric matrix

$B$  = a column matrix of 12 unknowns (variances)

$G$  = a column matrix of 12 computed sums of squares.

The coefficients for the components of variance, as presented in Table 3, are obtained in exactly the same manner as illustrated in the preceding section based on Model 4. However, it is possible because of the hierarchial classification of the data (as in Model 1, Table 3) to reduce the computations required by appropriate subtractions as is indicated in Table 3. This technique has been illustrated by King and Henderson (1954a).

## Heritability

The phenotypic of an individual can be represented in terms of the five causes of phenotypic variation in a linear form as follows:

$$P = G + D + I + E + \overline{EH}$$

where  $P$  = phenotype of the individual  
 $G$  = genic deviations  
 $D$  = dominance deviations  
 $I$  = epistatic deviations  
 $E$  = environmental deviations  
 $\overline{EH}$  = joint effects of heredity and environment.

This linear function can be written in terms of variances as,  $\sigma^2 P = \sigma^2 G + \sigma^2 D + \sigma^2 I + \sigma^2 E + \sigma^2 \overline{EH}$ , which assumes that all covariance terms are zero.

Heritability is defined by Lush (1948) in the broad sense as,

$$h^2 = \frac{\sigma^2 G + \sigma^2 D + \sigma^2 I}{\sigma^2 G + \sigma^2 D + \sigma^2 I + \sigma^2 E + \sigma^2 \overline{EH}},$$

and in the narrow sense as,

$$h^2 = \frac{\sigma^2 G}{\sigma^2 G + \sigma^2 D + \sigma^2 I + \sigma^2 E + \sigma^2 \overline{EH}}.$$

Heritability may be estimated from components of variance for sires, dams and full sibs by the method of intra-class correlation.

(a) Estimate from sires' component of variance:

$$h^2 = \frac{4S}{Q + S + D}.$$

This is sometimes referred to as heritability estimates from paternal half sib correlation.

(b) Estimate from dams' component of variance:

$$h^2_d = \frac{4D}{Q + S + D} .$$

(c) Estimate from sires' and dams' components of variance:

$$h^2_{sd} = \frac{2(S + D)}{Q + S + D}$$

Kempthorne (1955) has shown that (a) is a consistent estimate of:

$$\frac{1}{\sigma^2_P} \left\{ \sigma^2_A + 1/4 \sigma^2_{AA} + 1/16 \sigma^2_{AAA} + \text{etc.} \right\}$$

and (b) is a consistent estimate of:

$$\frac{1}{\sigma^2_P} \left\{ \sigma^2_A + \sigma^2_D + 3/4 \sigma^2_{AA} + 1/2 \sigma^2_{AD} + 1/4 \sigma^2_{DD} + 7/16 \sigma^2_{AAA} + \text{etc.} \right\}$$

where  $\sigma^2_P$  = phenotypic variance, and subscripts A and D refer to the additive and dominance deviations, respectively. For the case of (b) Kempthorne states, "the estimate  $h^2$  is valid only if the effects of genes are additive, and any type of deviation from additivity will cause the estimate to be inconsistent."

Maternal effects, which can be conceived as being of direct maternal influence and correlations of direct with transmitted effects, if present, will be included in the dams' component of variance.

Since the female is the heterogametic sex in birds, in the case of the analyses based on female progeny sex-linked effects will be included

in the sires' component of variance but not in the dams' component of variance.

Effects due to environmental correlations among paternal half sibs would be included in the sires' component of variance and effects due to environmental correlations among maternal sibs would be included in the dams' component of variance. Also, effects due to genotype-environment interactions, if present, would be included in the sires' and dams' components of variance.

### Phenotypic and Genetic Correlations

The analysis of covariance used to estimate covariance components parallels that used to estimate components of variance.

Methods for computing genetic correlations were developed by Hazel (1943).

The phenotypic correlation between traits may be estimated as follows:

$$r_{ij}^P = \frac{Q_{ij} + S_{ij} + D_{ij}}{\sqrt{(Q_i + S_i + D_i)(Q_j + S_j + D_j)}}$$

where Q, S and D are the full sibs', sires' and dams' components of variance or covariance respectively for the  $i^{\text{th}}$  and  $j^{\text{th}}$  traits.

The genetic correlations between traits may be estimated as follows:

(a) Estimate from sires' variance and covariance components:

$$r_{ij}^G = \frac{S_{ij}}{\sqrt{S_i + S_j}},$$

(b) Estimate from dams' variance and covariance components:

$$\hat{r}_{ij}^G = \frac{D_{ij}}{\sqrt{D_i + D_j}}, \text{ and}$$

(c) Estimate from sires' and dams' variance and covariance components:

$$\hat{r}_{ij}^G = \frac{S_{ij} + D_{ij}}{\sqrt{(S_i + D_i)(S_j + D_j)}}.$$

### Selection Indices

Smith (1936) derived an index for plant selection by the use of a discriminant function. Hazel (1943), utilizing a different approach, derived the theoretical details as well as the method of construction of a selection index. The method depends on assigning both genetic and economic weightings for the traits included in the index. Phenotypic and genetic correlations between the traits are also included in deriving the index.

The net merit of an individual is defined by Lush (1948) as:

$$G = f(G_1, G_2, \dots, G_n),$$

where  $G$  with a subscript is the genic value of the individual for a trait considered in the index. Expressing this in linear form,

$$G = a_1 G_1 + a_2 G_2 + \dots + a_n G_n \quad (1)$$

where the  $a$ 's are the relative economic values of the traits.



The index is a function of the observed traits and is defined as:

$$I = b_1 X_1 + b_2 X_2 + \dots + b_n X_n \quad (2)$$

where the X's are the phenotypic value for the traits, and the b's take whatever values will make  $r_{IG}$  (the correlation between I, the index value, and G, the genic value) a maximum.

The right hand sides of equations (1) and (2) written in the form of variances and covariances for the genotype and phenotypic values are equated in a series of "n" equations as follows (Smith, 1936):

$$\begin{aligned} a_1 \sigma_{G_1}^2 + a_2 \sigma_{G_1 G_2} + \dots + a_n \sigma_{G_1 G_n} &= b_1 \sigma_{P_1}^2 + b_2 \sigma_{P_1 P_2} + \dots + b_n \sigma_{P_1 P_n} \\ a_1 \sigma_{G_2 G_1} + a_2 \sigma_{G_2}^2 + \dots + a_n \sigma_{G_2 G_n} &= b_1 \sigma_{P_1 P_2} + b_2 \sigma_{P_2}^2 + \dots + b_n \sigma_{P_2 P_n} \\ &\vdots \\ a_1 \sigma_{G_n G_1} + a_2 \sigma_{G_n G_2} + \dots + a_n \sigma_{G_n}^2 &= b_1 \sigma_{P_n P_1} + b_2 \sigma_{P_n P_2} + \dots + b_n \sigma_{P_n}^2 \end{aligned} \quad (3)$$

where

$\sigma_{G_i}^2$  = genotypic variance of the  $i^{\text{th}}$  trait

$\sigma_{G_i G_j}$  = genotypic covariance between the  $i^{\text{th}}$  and  $j^{\text{th}}$  traits

$\sigma_{P_i}^2$  = phenotypic variance of the  $i^{\text{th}}$  trait

$\sigma_{P_i P_j}$  = phenotypic covariance between the  $i^{\text{th}}$  and  $j^{\text{th}}$  trait.

The equations in (3) can be outlined in matrix algebra symbols as follows:

$$GA = PB$$

where

$G$  = the genetic matrix of variances and covariances

$A$  = the matrix representing the economic weightings

$P$  = the phenotypic matrix of variances and covariances

$B$  = the matrix of unknowns representing the index coefficients.

The solution of the equations (3) is obtained as follows:

$$\text{let } GA = H$$

which can be written as,

$$P^{-1}H = P^{-1}PB$$

since

$$P^{-1}P = I$$

then

$$B = P^{-1}H.$$

The  $b$  values are the coefficients for the traits included in the index as given in (2).

The expected gain for the  $i^{\text{th}}$  trait when selection is based on index is given by (Morley, 1950),

$$\Delta G_i = \frac{\sum_j b_j \sigma_{G_i G_j}}{\sigma_I} \quad (4)$$

where

$\bar{L}$  = selection differential (in phenotypic standard units of the index)

$b_j$  = index value for the  $j^{\text{th}}$  trait

$\sigma_{G_i G_j}$  = genetic covariance between  $i^{\text{th}}$  and  $j^{\text{th}}$  traits

$\sigma_I$  = standard deviation of the index.

A selection index may be constructed which is designed to improve a single trait only but taking into account other traits. Correlated

traits are assigned an economic weight of zero and the trait in question is assigned an economic weight of one. As the accuracy of identification of a genotype for the desired trait is increased, the efficiency of selection for the given trait will be greater utilizing the index method.

This increase in efficiency for a given trait based on index selection relative to selection based on the trait alone may be estimated from the expected genetic gains as follows,

$$\frac{\Delta G_i}{\Delta G} = \frac{\text{Genetic gain in } i^{\text{th}} \text{ trait from index selection}}{\text{Genetic gain in } i^{\text{th}} \text{ trait when it is the sole criterion of selection}}$$

When the  $i^{\text{th}}$  trait is the sole criterion of selection, the expected genetic gain per generation is given by,

$$\Delta G_i = \bar{i} h^2 \sigma_p$$

$\bar{i}$  = selection differential (in phenotypic standard units of the trait)

$h^2$  = heritability of the trait

$\sigma_p$  = phenotypic standard deviation of the trait.

## SOURCE OF DATA

This study was based on a breeding experiment conducted at the Poultry Division, Central Experimental Farm, Ottawa, for the three years 1952 to 1954.

Data were obtained on a new breed developed at the station called the Broad Breasted White (Munro, 1946). This breed, hereafter designated B.B.W., was developed from crosses involving the Dark Cornish, White Leghorn, Light Sussex and the Rhode Island Red. The objective was to produce a meat breed incorporating desirable fleshing characteristics with white plumage and fast feathering.

Although this breed originated from a wide genetic base, the records available indicate that the breeding population in the developmental years prior to 1950 was at times relatively small. No attempt has been made to estimate the inbreeding resulting from the small population size as records covering these years were either not available or incomplete.

Progeny were secured from 15 individual male breeding pens in 1952 and from 20 individual pens in 1953 and 1954. Each pen contained 10 B.B.W. females. The males and females were assigned to the breeding pens at random with the one restriction that full sibs were not mated.

Each year 4 hatches were obtained. The first two hatches were assigned to Ottawa. The second two hatches were assigned to three farms, Ottawa, Ontario; Charlottetown, P.E.I.; and Lethbridge, Alberta. These are experimental farms of the Experimental Farms Service, Canada Department of Agriculture. All hatches were pedigreed and the assignments to the three farms were made at random within full sib families.

All chicks were raised under standard commercial broiler conditions to 12 weeks of age. Uniform management practices were followed as far as possible at all 3 locations. One square foot of floor space per bird was provided from one day of age and uniform feeding and watering standards were established for all locations. The same ration was used at the three locations. The ration was mixed by a commercial feed company at an eastern and western plant of the company. Ottawa and Charlottetown were supplied by the eastern mixing plant and Lethbridge by the western plant.

The data secured on the birds were as follows:

<u>Hatch No.</u>	<u>Farm</u>	<u>Data</u>
1 & 2	Ottawa	<p><u>Males:</u> Body weight at 6 and 12 weeks of age; breast angle at 12 weeks on live birds.</p> <p><u>Females:</u> Body weight at 6, 12, 24 and 52 weeks of age; breast angle at 12 weeks; sexual maturity; egg production to 500 days of age.</p>
3 & 4	3 Farms	<p><u>Males and Females:</u> Body weight at 6 and 12 weeks of age on live birds. Body depth, breast width, keel and shank length at 12 weeks of age on dressed birds.</p>

Body weight was obtained to the nearest 10 grams (decagrams). Breast angle was measured with a West Virginia angle meter in degrees (Clark and Cunningham, 1949). Body depth and breast width were measured with the Bird (1948) instrument in millimeters. Keel and shank length were measured with calipers to the nearest millimeter.

Sexual maturity was measured as days of age at the first recorded egg in the trapnest. Egg production records were secured on a five-day-a-week trap basis to 500 days of age.

## RESULTS

## Heritability Estimates

Heritability estimates for the various traits are presented in Tables 5a through 5k according to model number, year and sex where applicable.

The heritabilities for 6-week body weight are given in Table 5a; for 12-week body weight in 5b; for 24-week body weight in 5c; for 52-week body weight in 5d; for body depth in 5e; for breast width in 5f; for keel length in 5g; for shank length in 5h; for breast angle in 5i; for sexual maturity in 5j; and for hen-housed egg production in 5k.

There are a few cases, as seen in these tables, where the heritability estimates turned out to be negative. Although negative variances are obviously impossible, these estimates are nevertheless presented in order to indicate the range. Since negative variances are assumed to arise from sampling error, they were included in the means of combined estimates. A number of these negative estimates were obtained in the analyses of breast width (Table 5f). Apparently the heritability of this trait is extremely low. Accordingly, it is understandable that these negative estimates might frequently arise from sampling error. In the case of sexual maturity for 1954 (Table 5j), a negative estimate was also obtained. This estimate is widely divergent from the other estimates and the explanation does not appear to be sampling error.

Table 5a. Heritability of 6-week body weight

Model	Year	Sex	Method		
			4S	4D	2(S+D)
1	52	M	-.01	.54	.26
		F	.45	.55	.50
	53	M	.17	.11	.14
		F	.38	.29	.33
	54	M	.09	.54	.32
		F	.57	.38	.48
2	52	M	-.15	1.78	.82
		F	-.10	1.50	.70
	53	M	.38	.40	.39
		F	.60	.48	.54
	54	M	.13	1.16	.64
		F	.41	1.10	.75
3	52	M	.04	1.49	.76
		F	-.08	1.49	.71
	53	M	.33	.39	.36
		F	.59	.53	.56
	54	M	.18	1.12	.65
		F	.33	1.06	.70
1	Combined <sup>a</sup>	M	.08	.40	.24
		F	.47	.41	.44
2	Combined	M	.12	1.11	.62
		F	.30	1.03	.66
3	Combined	M	.18	1.09	.59
		F	.28	1.03	.66

<sup>a</sup>Unweighted means

Table 5b. Heritability of 12-week body weight

Model	Year	Sex	Method		
			4S	4D	2(S+D)
1	52	M	.32	1.16	.74
		F	.44	.53	.49
	53	M	.30	-.01	.15
		F	.40	.76	.58
	54	M	0	.75	.37
		F	.36	.56	.46
	52	M	.11	1.41	.76
		F	-.05	1.18	.57
	53	M	.41	.72	.57
		F	.74	.68	.71
	54	M	.15	.79	.49
		F	.21	1.13	.67
3	52	M	.27	1.24	.76
		F	.08	1.08	.58
	53	M	.41	.61	.51
		F	.82	.54	.68
	54	M	.20	.66	.43
		F	.14	.98	.56
1	Combined	M	.21	.63	.42
		F	.40	.62	.51
2	Combined	M	.22	.97	.61
		F	.30	1.00	.65
3	Combined	M	.29	.84	.57
		F	.35	.87	.61



Table 5c. Heritability of 24-week body weight of pullets

Model	Year	Method		
		4S	4D	2(S+D)
2	52	.22	.78	.50
	53	.92	.59	.76
	54	.19	.69	.46
3	52	.33	.73	.53
	53	.87	.67	.77
	54	.20	.83	.54
2	Combined	.44	.69	.57
3	Combined	.47	.74	.61

Table 5d. Heritability of 52-week body weight of pullets

Model	Year	Method		
		4S	4D	2(S+D)
2	52	.49	.45	.47
	53	.59	.56	.57
	54	.03	1.05	.54
3	52	.52	.41	.47
	53	.57	.65	.61
	54	.03	1.06	.54
2	Combined	.37	.69	.53
3	Combined	.37	.71	.54

Table 5e. Heritability of body depth at 12 weeks of age

Model	Year	Sex	Method		
			4S	4D	2(S+D)
1	52	M	.28	.78	.53
		F	.23	1.26	.75
	53	M	.35	.10	.22
		F	.05	.51	.49
	54	M	.13	.40	.27
		F	.37	.73	.55
Combined	M	.25	.43	.34	
	F	.22	.83	.60	

Table 5f. Heritability of breast width at 12 weeks of age

Model	Year	Sex	Method		
			4S	4D	2(S+D)
1	52	M	-.16	-.02	-.09
		F	.15	.14	.14
	53	M	.32	.72	.52
		F	.08	-.13	-.03
	54	M	.06	-1.15	-.54
		F	.19	-.27	-.04
	Combined	M	.07	-.15	-.04
		F	.14	-.09	.02

Table 5g. Heritability of keel length at 12 weeks of age

Model	Year	Sex	Method		
			LS	LD	2(S+D)
1	52	M	.64	.82	.73
		F	.69	.66	.67
	53	M	.34	.12	.23
		F	.10	.83	.46
	54	M	.27	.79	.53
		F	.17	.06	.12
Combined		M	.42	.58	.50
		F	.32	.52	.42

Table 5h. Heritability of shank length at 12 weeks of age

Model	Year	Sex	Method		
			LS	LD	2(S+D)
1	52	M	.49	.96	.73
		F	.44	.53	.48
	53	M	.14	.17	.16
		F	.53	.89	.71
	54	M	.08	.53	.31
		F	.50	.84	.67
Combined			.24	.55	.40
			.49	.75	.62

Table 5i. Heritability of breast angle at 12 weeks of age

Model	Year	Sex	Method		
			4S	4D	2(S+D)
2	52	M	.21	.32	.27
		F	.26	.64	.45
	53	M	.07	.93	.50
		F	.32	.38	.35
	54	M	.19	.61	.40
		F	.01	.13	.07
3	52	M	.30	.60	.45
		F	.34	.55	.45
	53	M	.16	.75	.45
		F	.23	.29	.26
	54	M	.11	.51	.31
		F	-.07	.05	-.01
2	Combined	M	.16	.62	.39
		F	.20	.38	.29
3	Combined	M	.19	.62	.40
		F	.17	.30	.23

Table 5j. Heritability of age at sexual maturity in pullets

Model	Year	Method		
		4S	4D	2(S+D)
2	52	.28	.71	.49
	53	.17	1.46	.82
	54	0	-.52	-.26
3	52	.30	.62	.46
	53	.25	.63	.44
	54	.15	-.38	-.12
2	Combined	.15	.55	.35
3	Combined	.23	.29	.26

Table 5k. Heritability of hen-housed egg production to 500 days of age

Model	Year	Method		
		LS	LD	2(S+D)
2	52	.24	.15	.20
	53	-.01	.58	.29
	54	.05	.09	.07
3	52	.31	.17	.24
	53	.05	.45	.25
	54	.03	.12	.07
2	Combined	.09	.27	.19
3	Combined	.13	.25	.19

The heritability estimates based on the dams' component are in general somewhat higher than those based on the sires' component. With the possible exception of the estimates for breast width, this is the case for all traits.

The unweighted means of the heritability estimates for the three years, based on twice the sires' plus dams' components, have been summarized in Table 6 according to model number and sex. The unweighted means of all estimates by sex and combined sexes are also given in this table. Body weight at 6 and 12 weeks of age were the only traits analyzed using the three models. It is of interest to note that the estimates for these traits, under Model 1, are somewhat lower than the estimates obtained under Models 2 and 3. This is especially true for 6-week weight. With the exception of sexual maturity, the unweighted estimates for the three years obtained under Model 2 (which assumes hatch effects) are in general of the same order as those under Model 3. The unweighted estimate for sexual maturity for the 3 years is .35 under Model 2 as compared to .26 for Model 3.

With the exception of the estimates for keel length and breast angle, heritability estimates for the females are slightly higher than the corresponding estimates for the males.

The estimates for body weight at 6, 12, 24 and 52-weeks of age, indicate a slight trend toward lower heritability with advancing age. In general, the heritability of body measurements reflecting skeletal development are about the same as those for body weight while those for body measurements, such as breast width and angle which reflect muscular development, are of a somewhat lower order. This seems especially true for breast



Table 6. Summary of heritability estimates based on sires' plus dams' components averaged over three years<sup>a</sup>

Trait	Sex	Model			Combined estimates <sup>a</sup>	
		1	2	3	by sex	both sexes
6-week body wt.	M	.24	.62	.59	.48	.54
	F	.44	.66	.66	.59	
12-week body wt.	M	.42	.61	.57	.53	.56
	F	.51	.65	.61	.59	
24-week body wt.	F		.57	.61		.59
52-week body wt.	F		.53	.54		.54
Body depth	M	.34			.34	.47
	F	.60			.60	
Breast width	M	-.04			-.04	-.01
	F	.02			.02	
Keel length	M	.50			.50	.46
	F	.42			.42	
Shank length	M	.40			.40	.51
	F	.62			.62	
Breast angle	M		.39	.40	.40	.33
	F		.29	.23	.26	
Sexual maturity	F		.35	.26		.30
Production index			.19	.19		.19

<sup>a</sup>

Unweighted means

width. The combined heritability estimate for this trait is close to zero. Breast angle, on the other hand, has a moderately high heritability estimate averaging .33 for the two sexes. The heritability for hen-housed egg production is moderately low averaging .19, while sexual maturity has a slightly higher heritability averaging .30 for the 3 years.

#### Phenotypic and Genetic Correlations

The phenotypic and genetic correlations obtained are presented in Table 7. These correlations are based on sires' plus dams' components of variance and covariance. The values presented are unweighted three year means of the individual yearly estimates, except where noted. In a number of cases, estimates for each year were not obtainable because the denominator was negative. Negative values were quite frequent in the case of breast width. Correlations involving this trait, presented in Table 7, are based on one year's data only.

In general, the correlations between different body measurements, reflecting skeletal size, are of a relatively high order. These body measurements also are quite highly correlated with body weight. The one exception to this is the low genetic correlation of .08 between 6-week body weight and keel length for males. This value appears somewhat inconsistent with the others.

The genetic correlations between body weights at different ages tend to decrease as the age interval increases. The trend is consistent for all estimates. As seen in the table, the correlations for females between

Table 7. Phenotypic and genetic correlations based on sires<sup>1</sup>  
plus dams' variance and covariance components  
averaged over three years<sup>2</sup>

Traits	Model	Males		Females	
		Pheno- typic	Gen- etic	Pheno- typic	Gen- etic
6-wk. x 12-wk.	1	.76	.71	.75	1.03
	2	.76	.87	.75	.91
6-wk. x 24-wk.	2			.50	.67
6-wk. x 52-wk.	2			.36	.50
6-wk. x Breast angle	2	.14	.28	.07	-.49 <sup>b</sup>
6-wk. x Breast width	1	.27	-.04 <sup>c</sup>	.19	.41 <sup>c</sup>
6-wk. x Body depth	1	.61	.75	.59	.73
6-wk. x Keel length	1	.55	.08	.54	.89
6-wk. x Shank length	1	.66	.63	.63	.81
6-wk. x Sexual maturity	2			-.13	-.31 <sup>b</sup>
6-wk. x Egg production	2			.02	-.06
12-wk. x 24-wk.	2			.73	.86
12-wk. x 52-wk.	2			.55	.76
12-wk. x Breast angle	2	.13	.23	.04	-.38 <sup>b</sup>
12-wk. x Breast width	1	.21	-.60 <sup>c</sup>	.26	.19 <sup>c</sup>
12-wk. x Body depth	1	.70	.75	.71	.67
12-wk. x Keel length	1	.59	.46	.71	.71
12-wk. x Shank length	1	.78	.61	.79	.87
12-wk. x Sexual maturity	2			.23	-.11 <sup>b</sup>
12-wk. x Egg production	2			-.02	.10

<sup>a</sup>Unweighted means of estimates for 3 years

<sup>b</sup>Unweighted means of estimates for 2 years only

<sup>c</sup>Unweighted means of estimates for 1 year only

Table 7. (Continued)

Traits	Model	Males		Females	
		Pheno- typic	Gen- etic	Pheno- typic	Gen- etic
24-wk. x 52-wk.	2			.65	.82
24-wk. x Breast angle	2			-.06	-.52 <sup>b</sup>
24-wk. x Sexual maturity	2			-.16	-.07 <sup>b</sup>
24-wk. x Egg production	2			.0	-.01
52-wk. x Breast angle	2			-.09	-.54 <sup>b</sup>
52-wk. x Sexual maturity	2			.03	.20 <sup>b</sup>
52-wk. x Egg production	2			.12	.10
Breast angle x sexual mat.	2			-.09	-.02 <sup>b</sup>
Breast angle x egg prod.	2			.09	.31 <sup>b</sup>
Breast width x body depth	1	0	-.53 <sup>c</sup>	.01	-.33 <sup>c</sup>
Breast width x keel length	1	.14	-.26 <sup>c</sup>	.14	-.71 <sup>c</sup>
Breast width x shank length	1	.12	.51	.13	.20
Body depth x keel length	1	.61	.53	.63	.68
Body depth x shank length	1	.69	.77	.71	.84
Keel length x shank length	1	.68	.42	.70	.84
Sexual maturity x egg prod.	2			-.35	-.39 <sup>b</sup>

6-week body weight and 12, 24 and 52-week body weights are .91, .67 and .50, respectively.

Breast width correlations with body weights and measurements varied widely. The genetic correlations between breast width and body weight at both 6 and 12 weeks are negative for males but positive for females. On the other hand, the genetic correlations between breast angle and 6 and 12-week body weights are moderately high but are positive for males and negative for females.

The genetic correlation between breast angle and sexual maturity is low and negative while the correlations of breast angle with hen-housed egg production are positive and of a somewhat higher order. The correlations between body weight and hen-housed egg production are all quite low. Correlations between body weight and sexual maturity are negatively correlated. However, the correlation is positive between 52-week body weight and sexual maturity.

#### Components of Variance (Model 4)

The components of variance are presented in Tables 8a through 8f, by sex and by year. Components for 6-week body weight, 12-week body weight, body depth, breast width, keel length and shank length are presented in Tables 8a, 8b, 8c, 8d, 8e and 8f, respectively. Many of the components are negative. These negative values were included in obtaining the arithmetic totals given at the bottom of each table. The negative values were assumed to be due to sampling error. The majority of these are associated with the first and second order interactions.

With the exception of breast width for 1952, the sum of the components of variance is higher for males than for females when compared on a within year basis.

In Table 9 combined estimates in terms of percentage of the total variance are presented for the 6 traits by sex. Negative components were treated as negative percentages (on a within year basis) and arithmetic means of the percentages for the 3 years are the values presented in Table 9. The underlying assumption in obtaining combined estimates in this manner was that the negative values were underestimates of the true variance and therefore simply reflect sampling error. The best unbiased combined estimate for the 3 years take the negative values into consideration.

The hatch component of variance represents only a small portion of the total variance for any of the 6 traits in Table 9. The percentage of the total variance due to farms is higher than that due to hatch. This is especially true in the case of body depth. Because of the nature of the effects which may be attributable to hatch and farm, these effects might be somewhat more prominent in some years than others. Examination of the absolute values of the components of variance in the tables (8a through 8f) for the individual traits suggests that this is true. For example, the farm components of variance for 12-week body weight, body depth and keel length in the 1952 analyses, are much greater than the 1953 or 1954 analyses.

In all cases, with the exception of the component for keel length in Table 9, the sires' component of variance is less than the dams' component of variance. Also, except for breast width for males, the sires'

and dams' components are positive. Further it appears that the sires' components tend to be lower for males than for females while the dams' components are not consistent for all traits in this respect.

The hatch x farm component in Table 9 constitutes generally, a higher percentage of the total variance than either the hatch or farm component. This is, in fact, an environment x environment interaction. The percentages for the other interaction components which are in effect hereditary x environment interactions varied widely. The large negative values associated with some of these components suggest that the sampling error of components of variance obtained in this manner are high.

#### Selection Indices

Four selection indices were constructed as follows:

Index A, 6 and 12-week body weights, body depth, breast width, keel length and shank length:

Index B, 6 and 12-week body weights and breast angle:

Index C, 6, 12, 24 and 52-week body weights, breast angle, sexual maturity and egg production:

Index D, 12-week body weight, breast angle and egg production.

Index A was based on data from Hatches 1 and 2, while Indices B, C and D were based on data from Hatches 3 and 4.

Unweighted means of the variances and covariances of the three years were used in the computations leading to the index coefficients. In a few instances this procedure would be expected to give slightly different

Table 8a. Components of variance for 6-week body weight

Component	Males			Females		
	52 <sup>a</sup>	53	54	52	53	54
Hatch	-9.4	9.0	7.1	-5.7	2.2	1.7
Farm	-5.2	-3.8	12.0	7.2	-0.8	7.8
Sire	1.1	2.9	-0.9	4.4	4.3	-0.5
Dam	44.6	8.7	19.8	11.8	5.4	14.2
H x F	35.3	9.6	11.8	16.0	7.1	3.3
H x S	-0.9	2.2	3.6	-1.1	0	2.6
H x D	-37.8	-5.4	2.7	5.2	2.5	-6.9
F x S	-1.6	1.7	4.0	1.3	3.1	10.2
F x D	-36.2	-14.7	-9.5	-9.2	-8.6	-12.5
H x F x S	0.5	-6.8	-7.2	-0.6	-4.0	-8.4
H x F x D	50.9	29.3	4.5	3.2	16.3	17.0
Remainder	46.9	40.8	46.7	24.3	34.8	30.1
Total	88.2	73.5	94.6	56.8	62.3	58.6

<sup>a</sup>Year



Table 8b. Components of variance for 12-week body weight

Component	Males			Females		
	52 <sup>a</sup>	53	54	52	53	54
Hatch	2.2	0.8	2.0	1.6	-8.4	-1.7
Farm	55.2	-0.3	5.5	27.1	-4.4	-5.3
Sire	35.0	23.2	-12.0	22.4	15.0	-0.7
Dam	8.9	10.1	49.7	32.8	8.3	56.3
H x F	-5.8	51.0	14.5	-2.7	31.5	10.8
H x S	-29.9	-2.2	30.7	-1.5	-13.4	9.6
H x D	-3.9	-18.2	-11.9	12.4	60.6	-20.4
F x S	-18.1	-7.0	18.6	-1.5	-11.1	34.4
F x D	71.4	-16.8	-25.8	-13.8	101.5	11.4
H x F x S	42.8	5.9	-44.8	-1.9	39.8	-42.4
H x F x D	18.1	55.3	74.2	-0.7	-236.2	-26.6
Remainder	170.3	196.6	154.0	133.5	200.8	190.1
Total	346.2	298.4	254.7	207.7	184.0	215.5

<sup>a</sup>  
Year

Table 8c. Components of variance for body depth

Component	Males			Females		
	52 <sup>a</sup>	53	54	52	53	54
Hatch	-0.9	1.6	1.3	0	2.7	0.5
Farm	16.4	6.9	6.2	11.3	7.6	5.5
Sire	3.7	0.9	-0.6	1.6	4.1	-0.3
Dam	5.4	5.4	5.6	7.3	1.3	6.1
H x F	2.6	0.6	2.5	1.5	-6.1	-0.6
H x S	-2.8	0.9	0.5	-0.8	-3.8	1.1
H x D	-3.8	-0.9	-1.8	1.1	0	-2.6
F x S	-2.3	2.0	1.0	-0.1	-4.6	2.6
F x D	-0.4	-7.0	-4.6	1.7	3.2	-2.2
H x F x S	4.2	-2.8	-0.2	0.3	9.8	-2.0
H x F x D	6.3	6.9	7.1	-4.5	-3.9	2.3
Remainder	17.8	17.3	11.9	15.7	17.2	14.8
Total	46.2	31.8	28.9	35.1	27.5	25.2

<sup>a</sup>  
Year

Table 8d. Components of variance for breast width

Component	Males			Females		
	52 <sup>a</sup>	53	54	52	53	54
Hatch	0	-0.4	2.0	-0.5	-0.9	1.5
Farm	0.5	-0.8	0.3	-0.7	-1.2	1.1
Sire	-0.2	0	-0.1	0	-0.1	0.5
Dam	3.3	1.0	1.4	1.6	2.1	0.3
H x F	0.4	2.5	2.3	1.3	3.4	1.6
H x S	-0.6	0.7	-0.3	1.1	0.7	-0.5
H x D	-1.5	-1.3	-0.4	-2.0	-2.6	0.4
F x S	-0.1	1.6	0.9	0.6	0.7	0.8
F x D	-6.1	0.7	-4.8	-1.2	-3.4	-1.3
H x F x S	0.4	-2.3	-0.8	-1.7	-1.6	-1.2
H x F x D	8.7	2.5	1.4	1.9	5.4	1.8
Remainder	4.6	7.1	12.2	9.4	7.5	7.3
Total	9.4	11.3	14.1	9.8	10.0	12.3

<sup>a</sup>Year

Table 8e. Components of variance for keel length

Component	Males			Females		
	52 <sup>a</sup>	53	54	52	53	54
Hatch	3.5	2.4	-0.3	-0.4	-0.1	-0.6
Farm	10.6	2.1	1.6	0.9	0.2	-0.1
Sire	9.2	1.8	0.9	3.5	2.1	1.1
Dam	0.3	-7.0	11.1	8.7	1.4	-0.4
H x F	-11.0	1.1	0.4	0.3	1.5	2.1
H x S	-5.8	2.9	2.7	2.2	-1.4	0.1
H x D	1.4	6.2	-5.0	-2.0	7.3	9.0
F x S	-10.0	8.2	1.3	1.5	-2.8	0
F x D	6.0	-4.5	-9.9	-4.0	3.9	15.9
H x F x S	17.0	-17.6	-3.7	-2.4	3.8	-0.5
H x F x D	-0.6	21.2	15.8	2.3	-5.8	-48.0
Remainder	16.6	16.1	12.1	19.1	17.6	46.8
Total	37.2	32.9	27.3	29.7	27.7	25.4

<sup>a</sup>  
Year

Table 8f. Components of variance for shank length

Component	Males			Females		
	52 <sup>a</sup>	53	54	52	53	54
Hatch	0.6	0.1	-0.8	-0.2	-0.8	-0.3
Farm	4.3	-1.5	2.5	2.0	-0.6	2.3
Sire	6.3	-0.3	-2.1	3.7	2.7	2.6
Dam	16.6	9.9	7.8	10.0	5.3	5.7
H x F	-0.9	3.4	1.8	0	2.4	0.4
H x S	-1.8	0	4.6	0.7	1.0	-0.2
H x D	12.7	-4.4	-3.1	-3.3	1.7	1.2
F x S	0.7	1.4	2.3	-0.5	-0.9	1.0
F x D	-26.2	-12.0	-3.1	-4.3	2.0	-1.8
H x F x S	0.6	-0.4	-4.1	-0.4	2.7	-1.3
H x F x D	31.7	14.1	-0.7	0.5	-3.0	2.0
Remainder	24.2	21.1	21.0	26.0	16.2	13.8
Total	43.4	32.0	26.1	34.2	28.7	25.4

<sup>a</sup>  
Year

Table 9. Components of variance for 6 traits, as percentage of the total variance (negative components treated as negative percentages, unweighted mean of percentages for 3 years)

Component	Sex	Trait					
		6-week weight	12-week weight	Body depth	Breast width	Keel length	Shank length
Hatch	M	3.0	0.6	2.6	2.6	5.1	-0.4
	F	-1.2	-1.5	3.8	-0.6	-1.4	-1.5
Farm	M	0.5	6.0	26.3	5.1	13.7	4.9
	F	8.2	2.6	27.3	-3.2	1.2	4.3
Sire	M	1.4	4.4	2.9	-0.1	11.2	1.8
	F	4.7	6.2	6.0	1.1	7.9	10.2
Dam	M	27.8	8.5	16.0	17.3	6.7	33.4
	F	17.8	16.5	16.5	13.1	10.9	23.5
H x F	M	21.8	7.0	5.4	13.5	-8.3	5.2
	F	15.1	7.1	-6.7	20.0	4.9	3.3
H x S	M	1.9	0.9	-0.5	-0.5	1.0	4.4
	F	0.8	-1.0	-3.9	4.8	1.0	1.5
H x D	M	-15.7	-4.0	-5.8	-9.9	1.4	-18.5
	F	0.4	9.4	-2.5	-14.3	18.4	0.3
F x S	M	1.6	-0.1	1.6	6.1	1.0	5.0
	F	8.2	3.7	-2.4	6.5	-1.7	0.2
F x D	M	-23.7	1.6	-12.9	-29.2	-11.2	-36.9
	F	-17.1	14.2	2.7	-19.0	21.0	-4.3
H x F x S	M	-5.4	-1.1	-0.2	-6.8	-7.0	-5.3
	F	-7.3	-0.4	9.4	-14.4	1.3	1.1
H x F x D	M	34.1	17.6	20.0	41.2	40.2	38.5
	F	20.2	-47.6	-5.9	29.4	-67.3	-0.4
Remainder	M	52.7	58.3	44.7	61.4	46.2	68.0
	F	50.0	90.7	55.5	76.7	104.1	62.3

results than one using the values on which the correlations (Table 7) were based. This discrepancy arises because a few of the correlations presented in Table 7 are based on one or two years' data only. However, the procedure used was felt to be satisfactory for combining these data and it had certain computational advantages.

Each of the four indices was examined from the standpoint of index selection designed to improve a single trait only. Individual indices were computed by assigning an economic weight of 1 to the given trait in the index and an economic weight of zero to all other traits in the index. This was done in turn for each trait in the index. The economic weightings and the index coefficients are presented in Table 10. In Index A 1, selection would be designed to improve 6-week body weight, in Index A 2, 12-week body weight, etc.

The expected genetic gain for a given trait under index selection was compared to the expected gain for the trait when the trait itself was the only criterion of selection. The ratio of the expected genetic gains from these two methods of selection can be used as a measure of the increase in efficiency when selection for improvement of a given trait is based on an index. These ratios for the individual traits in each index are presented in Table 11.

As seen in Table 11, the increases in efficiency range from one to 47 percent over all traits and indices. In Index A, selection for 6-week body weight (Index A 1, Table 10) shows an increase in efficiency of 47 percent for males and 15 percent for females. The corresponding increases in efficiency for 12-week body weight (Index A 2, Table 10) are 6 and 11 percent. The increases in efficiency for body depth and keel

Table 10. Economic weightings and selection index coefficients

Index no.	Sex	6-week weight	12-week weight	Body depth	Breast width	Keel length	Shank length	Breast angle	24-week weight	52-week weight	Sexual mat.	Egg prod.
A 1		1 <sup>a</sup>	0	0	0	0	0					
	M	1.65 <sup>b</sup>	1.0	4.68	.26	-4.36	2.25					
	F	1.09	1.0	-.03	1.03	-.75	.75					
2		0	1	0	0	0	0					
	M	-.38	1.0	-.34	-1.03	.08	-.15					
	F	1.19	1.0	1.68	-.68	-2.15	1.98					
3		0	0	1	0	0	0					
	M	.85	1.0	8.58	-10.67	.24	2.97					
	F	-.84	1.0	17.38	-6.88	-2.86	6.90					
4		0	0	0	1	0	0					
	M	2.18	1.0	-13.42	-2.16	5.90	-.51					
	F	.30	1.0	-1.92	-.50	-2.65	.86					
5		0	0	0	0	1	0					
	M	3.41	1.0	-1.21	-.88	12.71	-1.15					
	F	1.35	1.0	1.48	-4.95	4.61	2.95					
6		0	0	0	0	0	1					
	M	-8.57	1.0	1.21	-16.45	-.40	7.58					
	F	3.08	1.0	24.60	-11.69	-13.31	73.70					

<sup>a</sup>Economic weight<sup>b</sup>Coefficient



Table 10. (Continued)

Index no.	Sex	6-week weight	12-week weight	Body depth	Breast width	Keel length	Shank length	Breast angle	24-week weight	52-week weight	Sexual mat.	Egg prod.
B 1		1	0					0				
	M	7.33	1.0					1.36				
	F	4.41	1.0					-2.71				
2		0	1					0				
	M	1.00	1.0					.26				
	F	1.20	1.0					-1.23				
3		0	0					1				
	M	18.28	-1.0					163.72				
	F	-5.84	-1.0					21.64				
C 1		1	0					0	0	0	0	0
	F	.07	1.0					-1.42	-.09	-.01	-.12	-.04
2		0	1					0	0	0	0	0
	F	.04	1.0					-1.06	.04	.04	.04	.03
3		0	0					1	0	0	0	0
	F	-.30	-1.0					12.69	-.58	-.83	.53	.53
4		0	0					0	1	0	0	0
	F	.06	1.0					-3.58	1.66	.24	.16	.05
5		0	0					0	0	1	0	0
	F	-.02	1.0					-.38	.65	.90	.54	.05
6		0	0					0	0	0	1	0
	F	-.26	-1.0					5.49	.21	.88	4.76	.15

Table 10. (Continued)

Index no.	Sex	6-week weight	12-week weight	Body depth	Breast width	Keel length	Shank length	Breast angle	24-week weight	52-week weight	Sexual mat.	Egg prod.
C 7	F	0 .22	0 1.0					0 2.58	0 -.18	0 -.16	0 .18	1 .76
D 1	F		1 1.0					0 -1.06				0 .03
2	F		0 -1.0					1 4.76				0 .12
3	F		0 1.0					0 5.19				1 1.32
4	F		1 1.0					1 .45				1 .29
5	F		1 1.0					4 4.55				16 1.11
6	F		1 1.0					8 5.15				16 1.26
7	F		1 1.0					5 2.92				1 .18
8	F		3 1.0					10 .98				1 .21
9	F		4 1.0					16 1.37				1 .21
10	F		3 1.0					21 5.35				1 .45

Table 11. Increase in efficiency from index selection (in percent)

Trait	Index <sup>a</sup>					
	A		B		C	D
	M.	F.	M.	F.	F.	F.
6-Week body weight	47	15	2	7	1	
12-Week body weight	6	11	2	6	6	5
Breast width	-	-				
Body depth	11	4				
Keel length	9	19				
Shank length	2	3				
Breast angle			2	16	36	24
24-Week body weight					6	
52-Week body weight					12	
Sexual maturity					5	
Egg production					16	10

<sup>a</sup>The letter designation of the index refers to the traits incorporated in the index. The values given in the table are based on the individual indices as given in Table 10. For example, the values for 6-week body weight under Index A are based on Index A 1 (Table 10), for 12-week body weight in Index A 2, etc.

length are approximately of the same order as for 12-week body weight, while the increase in efficiency for shank length is only 2 to 3 percent. No values are given in the table for breast width since the heritability estimate for this trait was negative.

For Index B, the increases in selection efficiency are slightly lower for 6-week and 12-week body weights than in Index A.

The increases in efficiency for corresponding traits in Index C are slightly higher than in Index D. It is of interest to note that increases in efficiency for breast angle are fairly large, being 24 and 36 percent in Indices C and D, respectively.

As the three traits included in Index D are of great economic importance to the breeder of meat birds, indices were constructed incorporating these traits and assigning economic weights on the basis of economic considerations.

In the case of body weight, one pound increase in market weight was estimated to be worth approximately 14 cents in net returns to the producer (based on an average selling price in 1952-54 for live broilers of 28 cents on the Toronto, Ontario market and considering the cost of feed for producing this extra pound). For breast angle, economic weights were established on the basis of price differentials between market grades. From a sample of birds, graded according to the grade standards of the Canada Department of Agriculture, the mean difference in breast angle between market grade classes was found to be 2.3 degrees (see Table 16 for data classified by grade). The value of one egg increase in production was taken as 5 cents. Eggs produced for hatching purposes would have a slightly higher value than eggs produced for market purposes. In the case

of meat strains, layers would be maintained primarily for the production of hatching eggs.

In terms of units used in these analyses, the following are the values in cents used in assigning economic weights.

<u>Trait</u>	<u>Unit</u>	<u>Unit value in cents</u>
Body weight	decagram	.31
Breast angle	degrees	.43
Egg production	egg	5.0

Although the above values were the basic values used in assigning economic weights, other considerations were also felt to be of some importance in determining the economic weights to be used in constructing indices. For example, price differentials between market grades in commercial practice are not usually uniform. Therefore, the level of improvement of a strain (for breast angle as a criterion of market grade) would determine the economic value of further improvement. A further consideration in breeding for meat production is that a much larger proportion of the progeny are reared for market than for reproductive purposes. It was reasoned, therefore, that the economic value of traits such as body weight and breast angle are of greater economic importance to the breeder than a trait such as egg production.

The economic weights and the selection index coefficients for indices constructed on the basis of the above economic considerations are presented along with the other indices in Table 10. As these include the same traits included in Index D, they have been presented as extensions to this index as designated D 4 to D 10.

In Index D 4, equal economic weights were assigned to the three traits. In Index D 5, a price differential of 3 cents between market grades was assumed and in Index D 6, a price differential of 6 cents. Economic weights were assigned in Indices D 7, D 8, D 9 and D 10 by introducing arbitrary weighting factors to give greater weight in the index to body weight and breast angle relative to egg production. These weighting factors (the unit values in cents were weighted) were 20, 40 and 60 for Indices D 7, D 8 and D 9 respectively and in Index D 10, weighting factors of 40 for body weight and 80 for breast angle were used. The unit values for breast angle in Indices D 7 to D 10 were based on a grade price differential of 3 cents as in Index D 5.

The ~~expected~~ genetic gains for Indices D 1 to D 10 are presented in Table 12. The expected gains vary quite markedly depending on the economic weights used in the construction of the index. In Indices D 1, D 4, D 8 and D 9, the expected gains for breast angle are negative. All values for 12-week body weight are positive with the exception of Index D 2 in which selection is designed to effect maximum improvement of breast angle.

Table 12. Expected genetic gain by index selection for 12-week body weight, breast angle and egg production for different economic weights

Index no.	12-week body weight (decagrams)	Breast angle (degrees)	Egg production (number)
D 1	1 <sup>a</sup> 8.39 <sup>b</sup>	0 -.35	0 1.43
D 2	0 -6.14	1 1.26	0 2.84
D 3	0 1.51	0 .47	1 7.91
D 4	1 6.07	1 -.22	1 6.39
D 5	1 1.77	4 .45	16 7.90
D 6	1 1.49	8 .49	16 7.90
D 7	1 3.36	5 .32	1 7.49
D 8	3 6.22	10 -.18	1 5.94
D 9	4 5.83	16 -.08	1 6.05
D 10	3 2.10	21 .57	1 7.02

<sup>a</sup>Economic weighting

<sup>b</sup>Expected genetic gain

## DISCUSSION

## Heritability Estimates

Heritability ( $h^2$ ) is of considerable importance in formulating breeding plans. The expected response to selection is a function of the intensity of selection and heritability. For example, for simple individual selection this may be expressed as  $\Delta G$  (expected genetic gain)  $= i h^2$ , where  $i$  is in phenotypic units of the trait. Optimum selection methods and decisions with respect to alternate breeding plans also depend on  $h^2$ .

The heritability of a given trait in different populations or even in the same population at different times cannot be assumed to be constant (Lerner, 1950). It is also clear that different methods of estimating heritability are subject to different types of biases. Yet estimates obtained on different flocks and by different methods are of importance in establishing a general body of knowledge with respect to the heritabilities of different traits.

The heritability values reported in this study are in fair agreement with estimates for the same traits reported by others. One exception is the low estimate for breast width.

The instrument used for measuring breast width was that designed by Bird (1948). There are no reported heritability estimates of breast width measured with this instrument. However, using different measurement techniques, both Lerner et al. (1947) and Dillard et al. (1953) reported a heritability estimate of .21 for breast width. There is some indication



from the study of Blow and Glazener (1952) that the errors of measurement with Bird's instrument may be relatively great. These workers found rather poor agreement between live and dressed bird measurements taken with this instrument. Errors of measurement could be a possible explanation for the low heritability estimate of breast width measured with this instrument.

The heritabilities found in this study vary somewhat according to the model used, the sex of the birds on which the estimates were based and on the methods of estimation. It is of interest to consider the possible causes of these differences.

In the case of the mathematical models assumed in the analyses the choice of the model for the different traits was determined by the design of the experiment. Although all traits analyzed under Model 2 were also analyzed under Model 3, only two of the traits (6 and 12-week body weights) were analyzed under all 3 models. The estimates under Model 1 for these traits are somewhat lower than the estimates obtained under Models 2 and 3. The reason for this, other than sampling, is not clear. One explanation is suggested by the results of the analysis of these data according to Model 1. In this case hatch x farm interactions appear to be of some importance, especially for early body weight. Since the Model 1 analysis assumed only farm effects, the average effect of farms is probably all that has been removed in the analyses. In this case the environmental portion of the variance may tend to be slightly inflated.

Assuming that genetic x environmental interactions involving hatch effects are negligible, any differences in heritability estimates from

Models 2 and 3 would reflect differences due to hatch effects. Except for age at sexual maturity differences in the heritability estimates for the other traits under the two models do not seem important. The influence of hatch on the heritability of sexual maturity is in agreement with the report of King and Henderson (1954b). However, the inability to demonstrate hatch effects on heritability estimates for hen-housed egg production is not in line with the conclusions of King and Henderson even though the mean heritability estimates for hen-housed egg production were the same in both studies. The lack of agreement could result from differences in the two studies in length of hatching season. On each year only two hatches two weeks apart were secured in this study while the hatching season was spread over a much longer period of time in King and Henderson's study. There is little doubt that a longer hatching season would influence heritability estimates for all traits included in this study since growth as well as other traits are affected by season. These seasonal effects are more of the nature of fixed effects. Random effects on the other hand such as would be peculiar to a given hatch of birds raised under particular conditions are probably just as important in this study as they would be in data secured on hatches spread over a longer season.

Where estimates of heritability differed according to method of estimation the higher values were almost always associated with the dams' component. This could be due to several reasons. First, dams' component of variance includes maternal effects. Second, estimates of the dams' component includes sire-dam interaction variance. Third, an explanation given by King and Henderson (1954b) is that greater selection is practiced

on the sires. These workers suggested that the selected sires would have smaller additive genetic variance than would be expected from a less highly selected sample.

Evidence for maternal effects on traits considered in this study has been presented by different workers. Hazel and Lamoreux (1947) reported that 5 percent of the variation in housing body weight was due to maternal effects. Lerner and Cruden (1951) reported 15 percent of the variation in December body weight was due to maternal effects. These same workers found that 4 percent of the variation in body weight at broiler age, in the data reported by Lerner et al. (1947), was due to maternal effects. Brunson et al. (1955) reported maternal effects of 2 and 10 percent for 10-week body weight and breast angle, respectively. If it is assumed that the difference between the dams' and sires' components of variance are due to maternal effects, then estimates of maternal effects on body weight in this study average  $-.02$ ,  $.05$ ,  $.06$  and  $.08$  for 6, 12, 24 and 52-week body weight, respectively. Values for other traits were also of a similar magnitude. It is also of interest to note that these values show a progression with advancing age which is also characteristic of the values reported in the literature.

Whether any of these differences in the sires' and dams' components are due to interactions between sire and dam, or genic interactions, cannot be determined in these data. There are few reports in the literature on this subject. Hazel and Lamoreux (1947) found very little evidence of nicking in body weight or sexual maturity in a strain of White Leghorns. These workers point out, however, that possibly in their data (on a closed

flock) non-additive hereditary interactions may be an important source of variation among individuals without having much influence on family averages. Brunson et al. (1955) in a study involving two breeds, New Hampshires and Silver Oklabars, reported that 2 percent of the total variance in body weight and breast angle at 10 weeks of age was due to non-additive gene effects.

The sex differences in heritabilities found in this study are of some interest. Estimates for 6 and 12-week body weights, body depth and shank length were higher for females but estimates for keel length were higher for males. Except for 6-week body weight this is in agreement with the report of El-Tbiary and Shaffner (1951). In a more recent study by Godfrey and Goodman (1956) involving 10-week body weight and breast angle, no consistent sex differences in heritability were found. Estimates for breast angle were slightly higher for males than for females in this study.

The underlying reason for a possible sex difference in heritability is to some degree speculative. One explanation is that such differences are due to sex-linked effects. It is possible that a transformation of growth data to a different scale might remove any bias which may be introduced due to differential growth of the sexes. It is quite clear that the variances for the different traits are of a different order for males and females (Table 5a through 8f).

No sampling errors on the heritability estimates were obtained in this study. Osborne and Paterson (1952) worked out the standard error for estimates derived from components of variance for the case of equal subclass numbers. Farnsworth (1956) obtained good agreement with this method

in the case of unequal subclass numbers. Graybill et al. (1956) have presented a method for setting confidence limits on heritabilities obtained from components of variance for the equal subclass case. However, in these data, where farm and hatch effects (as in Models 1 and 3) were assumed, these techniques are not applicable.

### Genetic Correlations

Genetic correlations are of importance because they indicate what changes might be expected in one trait when selection is practiced for another and secondly, a knowledge of them may be utilized in improving the efficiency of selection.

For the most part the genetic correlations found in this study are in general agreement with previous reported estimates. Some exceptions are those involving breast width and breast angle. A few correlations between certain traits were obtained for which no estimates have been previously reported.

Because of the economic importance of breast development the disagreement between some of the correlations involving this breast width and angle and those reported in the literature is of some interest. The low heritability of breast width found in this study suggests that not much reliability could be placed on the correlation estimates. The genetic correlation between breast angle and 12-week body weight was positive for males but negative for females. This is not in agreement with the estimates reported by Godfrey and Goodman (1956). These workers reported an average genetic correlation between 9-week body weight and breast angle of .50,

which was positive for both sexes. This genetic correlation reported by these workers is somewhat higher than genetic correlations between body weight and breast width reported by Lerner et al. (1947) and Dillard et al. (1953). However, neither of these studies included estimates based on male and female progeny separately.

If it were assumed that the difference in sign in these correlations between males and females were real and not due to sampling error, the genetic explanation would be a matter of speculation. In a random breeding population in equilibrium genetic correlations are assumed to be due to the pleiotropic effects of genes. It could be assumed that sex-linked genes were responsible. Such a situation could lead to complications in a breeding program. Further estimates of these correlations are desirable as body weight and breast development are important economic traits in meat strains.

Among the correlations for which no previous estimates have been reported are those between breast angle and sexual maturity and egg production. In the case of sexual maturity this correlation was low and negative ( $-.02$ ) but with egg production it was somewhat higher and positive ( $.31$ ). A positive correlation between breast angle and egg production would be of some encouragement to the breeder interested in the development of meat strains.

#### Genotype-Environment Interactions

Genotype-environment interactions may be looked upon as an obstacle to selection for genetic improvement in performance over a range of

environments or conditions. Such interactions would lower the accuracy of selection. On the other hand breeding for best performance in given environments would require the development of many lines, each suited to a particular environment. Even then however, this would assume that the environmental factors responsible for the interaction could be specified.

In this study the analyses under Model 4 were primarily designed to determine the importance of genotype-environment interactions. In this model both hatch and farm effects were regarded as random variables. Although this was felt to be a valid assumption for purposes of this study, there could be cases in a study dealing with these effects where the combined effects of either hatches or farms might be considered partly fixed and partly random. Effects due to season associated with hatches, for example, might be considered as systematic effects and the data could be corrected for it. Constant factors such as latitude or average temperatures associated with farms might be considered as fixed effects. Abplanalp (1956) has dealt with many aspects of this problem in his study on hatch effects on production traits.

Whether true interactions between genotype and environment exist in these data is difficult to say. The components of variance appear to have a high sampling error. Therefore very little can be drawn in the way of conclusions. There are certain trends in the combined estimates for the three years that are worth noting. The values for hatch x sire and farm x sire interactions are somewhat more consistent than the other genotype-environment interactions. The farm x sire interactions are slightly greater than those for hatch x sire. In either case, the values are of

a low magnitude when expressed as a percentage of the total variance.

The results are of some interest from environmental effects on different traits. It appears that the environmental effects (hatches, farms and interaction) are greater for early body weight (6-week) than at market age (12-week). This is in agreement with the general observation that birds are more sensitive to environmental effect during the brooding period than they are during later stages of growth when compensatory growth often takes place. The large value for body depth associated with farms suggests that this measurement was not secured as uniformly as possible at the three farms.

There are few reports in the literature dealing with genotype-environment interactions for the traits included in this study. The evidence to date mostly based on egg production traits, suggests that genotype-environment interactions are not generally of any great importance under normal breeding operations. Further work might profitably be undertaken to investigate this problem further.

The statistical method used has much to commend it. It permits one to utilize all available data in obtaining estimates even with unequal subclass numbers which are so characteristic of breeding data. The estimation of sampling errors involved in this type of analysis is unsolved. It would appear that the chief shortcoming in the present study is the lack of sufficient numbers of progeny. However, the experimental design used was felt to be a realistic one as it involves two important factors under practical breeding operations.



## Selection Indices

Aside from their value in describing conformation and growth, measurements such as body depth, keel or shank length cannot be readily evaluated in economic terms. Their chief utility in a practical breeding program primarily would lie in their value in assessing the breeding value of the bird for traits of direct economic importance. Their value in this respect would of course have to be balanced against the cost of obtaining them.

The increases in efficiency utilizing these traits, with 6-week body weight + breast width, in an index designed to improve 12-week body weight were from 6 to 11 percent (males and females respectively). These values are not extremely high. They are however in good agreement with the value of 10 percent reported by Lerner et al. (1947) for an index incorporating shank length, keel length and breast width along with body weight.

The expected increases in efficiency by utilizing an index to improve breast angle appear to be quite encouraging with an estimated increase of efficiency of up to 36 percent. However, incorporating breast angle with 12-week body weight and egg production, in an index designed to improve all three traits (or net worth), results in negative gains expected for breast angle under certain economic weightings. This results from the negative genetic correlation between body weight and breast angle. It would be unlikely that a commercial breeder would be justified in considering such an index in the development of a meat strain. In commercial practice the weak points of a strain are not always considered in terms of their net worth. If the correlation between these traits is truly

negative, selection for simultaneous improvement in both traits will be a compromise. Further estimates of the genetic correlations between these traits are desirable.

There are few reports dealing with selection for body weight and breast development in the literature. Clark and Cunningham (1953) reported on a selection experiment covering eight years and concluded that breast width appeared to be more responsive to mass selection than body weight. In a recent study Abplanalp and Asmundson (1956) reported that after 5 generations of selection, that selection response in a line selected on the basis of an index for breast width was about 20 percent greater than selection in the line in which breast width was the only criterion of selection. These workers concluded that their results confirm the usefulness of selection indices. Further selection experiments along these lines would be desirable.

## SUMMARY

Performance data were obtained on a pedigreed flock of Broad Breasted Whites (a meat strain of fowl) over a three year period. The traits measured were body weights at 6, 12, 24 and 52 weeks of age; body measurements including breast angle, breast width, body depth, keel and shank lengths, at 12 weeks of age; age at sexual maturity and egg production to 500 days of age.

Each year four bi-weekly hatches were obtained. The chicks from the first two hatches were reared at one farm only. Chicks from the second two hatches were distributed at random within dam groups to three widely separated farms. All birds were reared as broilers to 12 weeks of age and except for females of the hatches reared at one farm only, were disposed of at that age. Six and 12-week body weights were obtained on all birds. All body measurements except breast angle were secured on birds from the hatches reared at three farms while breast angle was the only body measurement obtained on birds from the other hatches.

The hierarchal type of analysis of variance was used to obtain variance and covariance components. From these heritabilities for all traits as well as phenotypic and genetic correlations between a number of traits were estimated.

In addition to the foregoing analysis, the data secured on birds reared at the three farms were analyzed to obtain components of variance for all main effects (hatches, farms, sires and dams) as well as all first and second order interactions among these main effects.

All analyses were carried out on a within-year and within-sex basis where appropriate.

The heritabilities of 12-week body weight, breast angle and hen-housed egg production were estimated to be .56, .33 and .20, respectively. The heritabilities of body measurements, with the exception of breast width and angle, were found to be the same order as body weight. The heritability of breast width was estimated close to zero. The heritabilities of body weights at different ages were of the same order although there was some indication of a lower heritability with advancing age.

The genetic correlations between body weights, and also between body weights and skeletal body measurements, were in general of a high order. The genetic correlations between 12-week body weight and breast angle was negative (-.38) based on female progeny, and positive (.23) based on male progeny. Between egg production and 12-week body weight the genetic correlation was .10 and between egg production and breast angle .31.

The estimates of genotype-environment interactions from the factorial analyses were unrewarding. The number of birds available for these analyses was limited and it appears the sampling errors were too large to allow for any conclusions to be drawn with respect to these interactions. There was some evidence that hatch x farm (environment x environment) interactions may be important for early body weight. The analyses indicated that farm effects were more important for some traits than others and also farm effects were greater than hatch effects.

Selection indices combining different traits were constructed. The expected genetic gains, from selection on the basis of an index, for a given trait (index designed for improvement of given trait) and from selection when the trait itself was the only criterion of selection were compared. The increase in efficiency from index selection ranged from one to 47 percent over all traits and indices. The expected genetic gains for 12-week body weight, breast angle and egg production from indices constructed on the basis of economic considerations were computed.

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**APPENDIX**

Table 13. Means of meat and egg production traits of the Broad Breasted Whites for the three years 1952 to 1954

Trait	Sex	Farm	Hatch	Year					
				1952		1953		1954	
				n <sup>a</sup>	$\bar{x}$ <sup>b</sup>	n	$\bar{x}$	n	$\bar{x}$
6-week body weight (grams)	M	O	1	175	507	320	550	314	558
			2	202	538	249	506	183	576
			3	52	502	60	549	53	535
			4	47	566	44	477	66	512
		L	3	49	588	62	555	39	670
			4	45	555	49	469	55	562
		C	3	51	548	65	497	42	573
			4	42	441	50	498	53	547
		Combined farms	Combined hatches	663	531	899	513	805	567
	F	O	1	241	453	343	474	314	488
			2	190	467	257	451	181	489
			3	48	453	74	493	41	463
			4	60	504	70	430	56	469
		L	3	66	509	76	448	57	555
			4	63	503	66	409	54	501
		C	3	61	461	76	435	42	491
			4	54	394	55	447	59	482
		Combined farms	Combined hatches	783	466	1017	448	804	492
12-week body weight (grams)	M	O	1	175	1529	320	1632	308	1547
			2	201	1525	247	1566	182	1629
			3	52	1445	60	1437	53	1564
			4	47	1451	44	1385	66	1575
		L	3	49	1564	62	1599	39	1664
			4	45	1551	49	1432	55	1591

<sup>a</sup>Number of individual birds<sup>b</sup>Mean of trait

Table 13. (Continued)

Trait	Sex	Farm	Hatch	Year						
				1952		1953		1954		
				n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	
12-week body weight (grams)	M	C	3	51	1135	65	1165	42	1592	
			4	42	1390	50	1196	53	1504	
		Combined farms	Combined hatches	662	11487	897	1502	798	1583	
	F	O	1	241	1254	333	1284	309	1259	
			2	189	1217	252	1235	179	1301	
			3	48	1168	74	1164	41	1240	
			4	60	1181	70	1119	56	1273	
		L	3	66	1223	76	1230	57	1289	
			4	63	1250	66	1144	54	1264	
		C	3	61	1123	76	1176	42	1284	
			4	54	1148	55	1254	59	1218	
		Combined farms	Combined hatches	782	1196	1002	1201	797	1266	
Breast angle (degrees)		M	O	1	175	79.5	320	82.5	308	80.0
				2	202	78.2	249	81.9	182	79.6
			Combined hatches	377	78.9	569	82.2	490	79.8	
	F	O	1	241	79.7	323	83.2	309	80.2	
			2	189	78.3	246	81.7	179	79.6	
		Combined hatches	430	79.0	569	82.5	488	79.9		
Body depth (cms.)	M	C	3	52	9.03	60	9.30	53	9.01	
			4	47	9.18	44	8.96	66	9.00	
		L	3	49	9.70	62	9.62	39	9.72	
			4	45	9.74	49	9.43	55	9.44	
		C	3	51	9.06	65	9.07	42	9.51	
			4	42	8.70	50	8.95	53	9.06	



Table 13. (Continued)

Trait	Sex	Farm	Hatch	Year						
				1952		1953		1954		
				n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	
Body depth (cms.)	M	Combined farms	Combined hatches	286	9.24	330	9.22	308	9.29	
	F	O	3	48	8.44	74	8.71	41	8.54	
			4	60	8.64	70	8.38	56	8.47	
		L	3	66	8.90	76	8.94	57	8.96	
			4	63	9.16	66	8.87	54	8.94	
		C	3	61	8.40	76	8.50	42	8.68	
			4	54	8.31	55	8.56	49	8.59	
	Combined farms		Combined hatches	352	8.64	417	8.66	299	8.70	
	Breast width (cms.)	M	O	3	52	2.47	60	2.55	53	2.72
				4	47	2.28	44	2.36	66	2.29
L			3	49	2.48	62	2.62	39	2.53	
			4	45	2.48	49	2.34	55	2.55	
C			3	51	2.54	65	2.54	42	3.00	
			4	42	2.58	50	2.69	53	2.75	
Combined farms		Combined hatches	286	2.47	330	2.52	308	2.64		
F		O	3	48	2.51	74	2.44	41	2.67	
			4	60	2.30	70	2.21	56	2.28	
		L	3	66	2.44	76	2.47	57	2.49	
	4		63	2.45	66	2.21	54	2.42		
	C	3	61	2.36	76	2.37	42	2.82		
		4	54	2.48	55	2.59	59	2.60		
Combined farms		Combined hatches	352	2.42	417	2.38	309	2.55		

Table 13. (Continued)

Trait	Sex	Farm	Hatch	Year					
				1952		1953		1954	
				n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Keel length (cms.)	M	O	3	52	9.58	60	9.35	53	9.64
			4	47	9.80	44	9.15	66	9.66
		L	3	49	9.94	62	9.77	39	9.87
			4	45	9.94	49	9.39	55	9.91
		C	3	51	9.54	65	9.46	42	9.99
			4	42	9.39	50	9.28	53	9.79
	Combined farms		Combined hatches	286	9.70	330	9.40	308	9.81
	F	O	3	48	8.78	74	8.76	41	8.95
			4	60	8.95	70	8.67	56	8.99
		L	3	66	9.07	76	8.97	57	9.07
			4	63	9.10	66	8.67	54	9.14
		C	3	61	8.94	76	8.85	42	9.37
			4	54	8.89	55	8.97	59	9.07
	Combined farms		Combined hatches	352	8.96	417	8.82	309	9.10
Shank length (cms.)	M	O	3	52	10.58	60	10.84	53	10.92
			4	47	10.59	44	10.47	66	11.07
		L	3	49	11.04	62	10.81	39	10.97
			4	45	10.94	49	10.49	55	10.81
		C	3	51	10.89	65	10.49	42	11.38
			4	42	10.73	50	10.64	53	11.16
	Combined farms		Combined hatches	286	10.80	330	10.62	308	11.05

Table 13. (Continued)

Trait	Sex	Farm	Hatch	Year					
				1952		1953		1954	
				n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$
Shank length (cms.)	F	O	3	48	9.45	74	9.64	41	9.81
			4	60	9.54	70	9.42	56	9.92
		L	3	66	9.71	76	9.55	57	9.74
			4	63	9.83	66	9.37	54	9.65
		C	3	61	9.78	76	9.52	42	10.08
			4	54	9.73	55	9.77	59	9.98
		Combined farms	Combined hatches	352	9.67	417	9.55	309	9.86
24-week body weight (gms.)	F	O	1	236	1996	323	2082	182	2090
			2	179	1922	246	2035	134	2063
			Combined hatches	415	1964	569	2061	316	2078
52-week body weight (grams)	F	O	1	216	2540	278	2634	169	2748
			2	153	2489	138	2700	122	2717
			Combined hatches	369	2519	416	2656	291	2735
Sexual maturity (days)		O	1	229	193	292	193	175	197
			2	175	198	149	195	129	201
			Combined hatches	404	195	441	194	304	199
Egg <sup>c</sup> production (number)	F	O	1	229	89	292	109	175	97
			2	175	93	149	107	129	91
			Combined hatches	404	86	441	108	304	94

<sup>c</sup>5-day-a-week trapnest figures

Table 14. Analysis of variance and expected mean square (Model 4, equal subclass case)

Source of variation	d.f.	Expected mean square											
		$\sigma^2_e$	$\sigma^2_{hfd}$	$\sigma^2_{hfs}$	$\sigma^2_{fd}$	$\sigma^2_{fs}$	$\sigma^2_{hd}$	$\sigma^2_{hs}$	$\sigma^2_{hf}$	$\sigma^2_d$	$\sigma^2_s$	$\sigma^2_f$	$\sigma^2_h$
Hatch	h-1	1	e	de			fe	fde	sde				fsde
Farm	f-1	1	e	de	he	hde			sde			hsde	
Sire	s-1	1	e	de	he	hde	fe	fde		hfe	hfde		
Dam w/i S	s(d-1)	1	e		he		fe			hfe			
H x F	(h-1)(f-1)	1	e	de					sde				
H x S	(h-1)(s-1)	1	e	de			fe	fde					
H x D w/i S	(h-1)s(d-1)	1	e				fe						
F x S	(f-1)(s-1)	1	e	de	he	hde							
F x D w/i S	(f-1)s(d-1)	1	e		he								
H x F x S	(f-1)(s-1)(h-1)	1	e	de									
HxFxD w/i S	(h-1)(f-1)s(d-1)	1	e										
Remainder	hfsd(e-1)	1											
Total	hfsde-1												

Table 15. The actual and maximum possible number of filled subclasses for data analyzed under Model 4 (Hatches 1 and 2)

Subclass	Sex	Year					
		1952		1953		1954	
		Number <sup>a</sup> of sub- classes	Number of sub- classes filled	Number of sub- classes	Number of sub- classes filled	Number of sub- classes	Number of sub- classes filled
Hatch	Males	2	2	2	2	2	2
Farm		3	3	3	3	3	3
Sire		14	14	19	19	19	19
Dam		87	87	105	105	106	106
H x F		6	6	6	6	6	6
H x S		28	28	38	37	38	35
H x D		174	133	210	156	212	151
F x S		42	41	57	54	57	51
F x D		261	183	315	212	318	205
H x F x S		84	78	114	95	114	89
H x F x D		522	234	630	271	636	264
Total			286		330		308
Hatch	Females	2	2	2	2	2	2
Farm		3	3	3	3	3	3
Sire		14	14	19	19	19	19
Dam		88	88	115	115	112	112
H x F		6	6	6	6	6	6
H x S		28	28	38	37	38	35
H x D		176	136	230	175	224	162
F x S		42	41	57	54	57	53
F x D		264	196	345	254	336	215
H x F x S		84	81	114	99	114	94
H x F x D		528	259	690	333	672	263
Total			352		417		309

<sup>a</sup>Refers to the maximum number of subclasses, if every dam had at least one progeny in each hatch and at each farm

Table 16. Differences between means for 6 and 12-week body weight and breast angle for birds classified by grade<sup>a</sup>

Sex	Year	Number of birds		6-week body wt. (gms.)	12-week body wt. (gms.)	Breast angle (deg.)
		Grade A	Grade B			
Males	52	62	33	-28 <sup>a</sup>	-16	3.5 <sup>**</sup>
	53	48	56	-51 <sup>*</sup>	-87 <sup>*</sup>	2.8 <sup>**</sup>
	54	68	51	15	36	3.5 <sup>**</sup>
	Combined years			-21	-22	3.3
Females	52	85	23	14	14	2.3 <sup>**</sup>
	53	82	61	-13	-15	2.8 <sup>**</sup>
	54	69	28	-40 <sup>*</sup>	10	1.7 <sup>*</sup>
	Combined years			-13	3	2.3

<sup>a</sup>Mean of birds classified Grade A - mean of birds classified Grade B

<sup>\*</sup>Significant at the P 0.05 level

<sup>\*\*</sup>Significant at the P 0.01 level